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Carnivore Competition and Resource use in the Serengeti Ecosystem of Tanzania

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CARNIVORE COMPETITION AND RESOURCE USE IN THE SERENGETI ECOSYSTEM OF TANZANIA

by

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of the requirements for the degree

of

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This monograph grew out of questions that arose during my two decades of acquaintance with East Africa's flora and fauna. During five of those years Lory Herbison Frame and I lived among and observed the wildlife in Tanzania's Serengeti ecosystem, where we were studying the ethology and ecology of cheetahs and African wild dogs.

When I returned to Utah State University to write the results of my cheetah research, I encountered a faculty whose interests lay heavily in community ecology. Consequently, discussions with Frederic H. Wagner, James A. MacMahon, Barrie K. Gilbert, David R. Balph, and others prompted me to examine the Serengeti carnivore data from a synecological perspective.

Since the 1950's, numerous field researchers have studied the Serengeti's larger species of Carnivora in detail. However, few attempts have been made thus far to draw together the current knowledge of these individual species, to describe how they coexist in one complex and dynamic community. This monograph, therefore, is my attempt to compile, synthesize, and relate to community theory that which currently is known about the Serengeti's large and medium-sized carnivores. I have tried to bridge the gap between the constraining logistical and methodological realities faced by field workers and the unbounded realm of the theoreticians. The result may be viewed by some as a crude first approximation (and it is), but it helps to define the enormous task that lies ahead. My hope is that this work will serve as a focus for future researchers by showing two directions for

improvement: (1) more-consistent and meaningful cross-species data collection, and (2) more-precisely stated community models that are testable.

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George Walter Frame

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ABSTRACT

Carnivore Competition and Resource Use
in the Serengeti Ecosystem of Tanzania

by

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Utah State University, 1986

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Coexisting ungulate-eating carnivores--lion, spotted hyena, cheetah, leopard, African wild dog, black-backed jackal, common jackal, and six species of vulture--are examined in East Africa's Serengeti ecosystem. Niche similarities year-round, by season, and by location are described using food, habitat, time of hunting, and other variables. Intraspecific niches of cheetah sex, age, and social groups show that male coalitions differ most from the others in hunting behavior and habitat use. Tests using the carnivore data failed to support hypotheses about niche breadth variation, niche overlap variation, range of food items, and niche inclusion. Densities of the five largest Carnivora in the 35,500 square kilometer ecosystem are 0.513/sq km; including the two jackals gives a density of 1.55/sq km. Their prey--30 ungulate species--are 84.85/sq km. Prey and predator ratios suggest that the Serengeti Plains in 1977 had a three-fourths

decrease in relative abundance of prey to predators from wet season to dry season. Year-round the Ngorongoro Crater had a prey:predator ratio slightly larger than that of the dry season Serengeti Plains. Literature review suggests that cleptoparasitism and direct killing are very important forms of interference competition among and within carnivore species. Evidence for exploitation competition is scant, but is inferred because local environments are unpredictable for carnivores. Analysis of body sizes fails to support the hypothesized ratios of 2.0 for body weight and 1.28 for linear dimensions. Three methods of calculating multidimensional niche metrics (product, summation, and projection) are compared. Apparently the Serengeti's carnivores coexist because of their behavioral flexibility in an unpredictable environment. Niche descriptions were of little help in assessing the foci for potential and real competition among carnivores. Only the direct observations of interference competition in long-term field studies identified where competitive interactions are occurring with sufficient intensity to provide a numerical response in a population. Spotted hyenas sometimes competitively exclude African wild dogs locally. Management for a high abundance and diversity of carnivores probably requires maintaining high densities of prey and varied habitats. Specific recommendations are made for cheetah and African wild dog conservation.

(394 pages)

CHAPTER I

INTRODUCTION

1.1 The Question

With seven species of large mammalian predators and 11 species of scavenging birds, East Africa's Serengeti ecosystem is unusually rich in carnivores. They feed on a common resource of 30 species of large herbivorous mammals, which suggests considerable potential for competition. How, then, do so many ungulate-eaters coexist in the Serengeti?

In search of an answer, three lines of investigation are pursued here. They are: a description of similarities in the ways that carnivores use the resources, an evaluation of the extent of competition, and an assessment of competition's influence on the carnivore community structure. Because competition is the common thread throughout, the concept must be reviewed and defined before the Serengeti's carnivores can be examined in detail.

1.2 The Nature of Competition

Competition occurs when individuals, within or between species, use a resource that is limited. If a resource is scarce, some individuals will fail to obtain sufficient amounts to survive or reproduce to the extent that they are genetically capable. Or, if an abundant resource is made locally or momentarily unavailable by a competitor, the losing individual will experience reduced efficiency

in obtaining or using it. Both conditions--the restricted availability of resources and the changed efficiency in using them--are likely to affect the genetic fitness (sensu E.O. Wilson 1975:585) of individuals, and cause a response in the numbers or character of their deme and perhaps their population.

Competition is very difficult to measure. An organismic response--either ecological, physiological, or behavioral--is important in identifying the existence of competition. These responses sometimes are measurable as niche shifts or population changes, either of which may be acceptable evidence of competition. A third measure of competition is aggressive interaction between individuals of the same or different species. The exploitation and interference competition, to which these three measures pertain, are described in the remaining sections of this chapter. They are discussed in terms of their occurrence among and within species. This will provide the framework for investigating the carnivores in the Serengeti ecosystem.

1.2.a Exploitation and Interference Competition

Competition can take the form of either exploitation or interference, although these two forms are not always clearly distinct. Exploitation competition occurs through the inequitable use of a finite resource. It is more difficult to demonstrate than is interference competition. Generally, to prove the existence of exploitation competition, a resource must be shown to be in limited supply to the extent that an organism, in the presence of another organism using the same resource, does not obtain an adequate amount for survival and

reproduction.

Interference competition, in contrast, is easily recognized by aggressive interactions. It is often direct, ranging from the simple appropriation of food, space, reproductive opportunity, or some other needed resource, to outright death for the loser or its offspring. It can also be indirect, as in the production of toxins, or in avoidance (Bock 1970; Morse 1974; Pianka 1970:174-175). If an organism expends more of its time, matter, or energy in the avoidance of interference, it reduces the amount left for maintenance and reproduction (Connell 1975; Pianka 1978:174-175; D.S. Wilson 1980:108-114). Even if a resource is not in short supply, its temporary local removal by a competitor can increase the costs (Thomson 1980). Either way--directly or indirectly--the organism suffers from the competition.

As is true of exploitation competition, the interference competition intensifies in times or places of resource scarcity. Aggressive encounters are more common or severe during predictable seasonal shortages of critical resources, as well as during the unpredictable shortages that occur in variable environments (Wiens 1977; Dunham 1980; D.C. Smith 1981). For example, hunger sometimes increases aggressive behavior in organisms ranging from hermit crabs (Hazlett 1966) to the Serengeti's large carnivores (G. and L. Frame 1981), although aggression is not to be confused with hunting behavior. Hunger does, however, lower the stimulus threshold for killing prey (Lorenz and Leyhausen 1973:221), and sometimes the inferior competitor becomes the prey. Interference may be an alternative to being an efficient exploiter of resources (Case and Gilpin 1974). If an animal cannot outperform its competitor for a limited resource, it might

instead attack the competitor, either to chase it away or take its food, or even to eat the competitor. Interference competition sometimes is the only kind of competition that is detectable (Schoener 1982). These kinds of aggressive interactions between individuals, both among and within species, are common in the Serengeti carnivores.

1.2.b Competition Among Species

Interspecific competition can occur directly between the indivuduals of two species, or it can come simultaneously from individuals in many species (MacArthur 1972:29; Davidson 1980), as might be expected to be occurring among the Serengeti's many carnivores. Competition sometimes occurs among the individuals of very different taxa, e.g. rodents and ants (J.H. Brown et al. 1979).

Interspecific competition among vertebrates often affects both sexes and all ages. Among lizards, however, competition was shown to be sex and age specific (Schoener 1968; D.C. Smith 1981).

When many species occur together, their niche hypervolumes and niche overlaps usually are reduced, i.e. contractions and shifts in resource use are expected to occur to minimize competition (Rappoldt and Hogeweg 1980). Niche compressions such as these have been shown to occur, for example, among lizard species (Pianka 1974) and among bird species (Williams and Batzli 1979a). The cumulative force of competition from several other species can drive out a vulnerable species (Giller 1984:17). So, even if pairwise niche overlaps are small, taken together they can be of decisive importance to an inferior competitor, given that a critical resource is in short supply.

Interspecific competition generally is accepted to be an important

driving force of natural selection (e.g. Diamond 1978), although there also are arguments that its importance is only slight (e.g. Wiens 1977; Simberloff 1982). Among species the long-term effect of competition might become apparent as character displacement (W.L. Brown and E.O. Wilson 1956). At the deme level, characters and numbers evolve in response to competitors regardless of the trend of the population containing the deme (Ayala 1971). Because the Serengeti carnivore community has existed for a very long time, the existing carnivore species might be evolving divergent features as a result of differential survival and reproduction in the competitive environment.

1.2.c Competition Within Species

Competition is important to individuals in the universal struggle to pass on their own genes. Individuals act not to perpetuate their species, but instead they strive to maximize their own reproductive success or that of their kin (Maynard Smith 1964; W.D. Hamilton 1971; Trivers 1985:20) Consequently, the same study methods of competition and niche dynamics that are used for comparing species and populations should be useful for studying individuals and social groups. The numerical response in this case might apply to kin lines, social groups, or demes. MacMahon et al. (1981) discussed the individual niche concept.

Intraspecific competition, either interference or exploitation, hinders conspecifics by lowering their relative number of reproducing offspring (J.L. Brown 1964). Female primates, for example, affect the reproductive success of others in their social group (Blaffer Hrdy 1981:96-130). In the extreme, such behavior manifests itself as direct

killing of adults and young (Hausfater and Blaffer Hrdy 1984). The same occurs among the Serengeti's African wild dogs (H. and J. van Lawick-Goodall 1970; L.H. Frame et al. 1979; G. and L. Frame 1981). When food or habitat resources are limiting, this selfish tendency might manifest itself as the defense of a super-territory (Verner 1977) to monopolize resources, although there are theoretical arguments to the contrary (Tullock 1979). The use of deceit, too, can affect the balance of a competitive relationship and thereby confer differential benefits within a species (Otte 1974, 1975; Krebs and Dawkins 1984; Alcock 1984:452-453).

Competition among sex, age, or kin groups often increases the variety of resources used by a population (Pianka 1978:184). Differential use of resources by the individuals of different sex and age classes has been described for fishes (Clarke 1977), chameleons (Hebrard and Madsen 1984), salamanders (Krzysik 1979), lizards (Creusere and Whitford 1982), birds (Storer 1966; J.B. Williams 1975), wapiti (Boyd 1978:17), African buffalos (Sinclair 1977), moose (Brazell 1981), bighorn sheep (Shank 1982), red deer (Clutton-Brock et al., 1982), and foxes (Storm 1965), just to name a few. In the Serengeti ecosystem, the sex and age classes of African lions use different resources (Schaller 1972; Bertram 1978). Each sex, cohort, kin line, or type of social group thus might be thought of as having a different niche. Some of these within-species differences must have evolved as a result of interference and exploitation competition.

Intraspecific competition is evolutionarily important (O.L. Smith et al. 1975). The short-term result of interference competition among conspecifics is deprivation of limited resources such as food, space,

and especially mates through agonistic behaviors or outright killing (Darwin 1859). Aggressive interactions such as these are commonly observed within some of the Serengeti's carnivore species (Bertram 1979). The long-term result is a change in gene frequency (Thomson 1980), an example of which is sexual dimorphism (Darwin 1871).

Competition within a species usually is more intense than competition from outside, so the abundant species is likely to be driven to genetic differentiation (McNaughton and Wolf 1970:137). The cumulative effect of competition from conspecifics, and from other species, must drive inferior kin lines to extinction.

In the following chapters, competition is considered first among species, and then it is considered among individuals and their social groups. This distinction is necessary, because factors that are favorable to a species' population are not favorable to all the individuals within that population.

1.3 Definitions

Before proceeding, several terms as used in this study must be defined to avoid semantic difficulties. They are:

Carnivore--Any vertebrate species, or individual, for which vertebrate flesh provides the major source of energy during adult life.

Carnivora--One or more species of the mammalian Order Carnivora. Some of the smaller Carnivora feed mainly on invertebrates, and are not carnivores as defined above.

Community--An assemblage of coevolutionarily interacting populations connected by the effects of one or more populations on the demography or genetic constitution of the others (sensu MacMahon et al.

1978). By this standard, it seems a safe assumption that all the Serengeti's Carnivora and their prey are part of one dynamic community.

Competition--Any direct or indirect interaction among organisms that are behaving in a similar manner, which reduces the genetic fitness of an individual or decreases population size. The interaction is assumed to be the direct or indirect result of using a resource that is in short supply at least temporarily. If other explanations can be discounted, the existence of competition is inferred from behavioral responses, niche shifts, changes in population size or structure, or shifts in gene frequency. Competition occurs within and among species.

1.4 Objectives

In search of answers to the question of how so many large mammalian and avian carnivores are able to co-exist in the Serengeti ecosystem, I established the following eight objectives:

(1) Describe the general ecological relationships that exist among the carnivores to identify their similarities in resource use. This requires beginning with a description of the ecosystem (Chapter Two) and the methods to be used (Chapter Three). The analyses use clustering, calculating niche breadths and overlaps, and drawing histograms of resources that are used differentially by the carnivores. These niche relationships are described using my own field data and the published and unpublished data of other researchers. Year-round interspecific niches are examined first (Chapters Four and Five).

(2) Search for indications that, among species, resources are sometimes limiting. The first step is to estimate prey and predator densities by season and by location, calculate their ratios, and

compare the results with other ecosystems in Africa (Chapter Six). Comparisons of niche similarities among carnivore species are made by season (Chapter Seven) and by location (Chapter Eight), to assess food availability. These provide comparisons of similarities in resource use in these different conditions.

(3) Examine the evidence for competitive exclusion, to provide indications that coexistence is not always possible (Chapter Nine).

(4) Review the literature for examples of interference competition among and within the Serengeti's carnivore species. Evaluate which species are involved in the most intense interference competition (Chapter Ten).

(5) Describe similarities in resource use among sex, age, and social groupings within a carnivore species. The cheetah is used as an example (Chapter Eleven).

(6) Examine several of the most popular models of community interactions to see if they are descriptive of the Serengeti carnivores. The hypotheses to be tested pertain to niche breadth variation, niche overlap variation, range of food items, peak of capture success, and niche inclusion (Chapter Twelve).

(7) Test for character displacement as a possible evolutionary response to competition among the Serengeti's carnivore species (Chapter Thirteen).

(8) Evaluate the importance of competition among the Serengeti carnivores in both the proximate and evolutionary perspectives, discuss the usefulness of the several niche methods and models in wildlife management, and recommend a management strategy for conserving carnivores, particularly the cheetah and African wild dog (Chapter

Fourteen).

When all of these objectives have been addressed, it is hoped that we will be closer to understanding how so many carnivores can coexist in the Serengeti ecosystem.

CHAPTER II

THE SERENGETI ECOSYSTEM

2.1 Physical Description

The Serengeti ecosystem lies about 500 km inland from the Indian Ocean (Fig. 2.1). The ecosystem covers an area of about 35,500 sq km (Bradley 1976), and is contained largely within the administrative boundaries of the Serengeti National Park and the Ngorongoro Conservation Area, Tanzania, and within the Masai Mara Game Reserve, Kenya (Fig. 2.2). The bounding coordinates are 1°15' to 3°26' south latitude and 33°52' to 35°42' east longitude. The Serengeti's landforms were described by Gerresheim (1974). Most of the ecosystem lies 1,200 to 1,800 m above sea level (Kruuk 1972a:12), extending from the Crater Highlands in the east to Lake Victoria in the west.

The boundaries of the ecosystem generally are accepted to be defined by the movements of the migratory ungulates, particularly the wildebeest, zebras, and topi, but many other large herbivores are abundant within this same area. The carnivore and herbivore components of the ecosystem are described in Sections 2.2 and 2.3. Scientific names of the mentioned Serengeti mammals and birds are presented in Appendices A and B, respectively.

Most of the ecosystem's vegetation is a mosaic of Acacia woodlands and treeless grasslands. At least 25% of the ecosystem is grasslands. The 12,800 sq km Serengeti National Park and 8,290 sq km Ngorongoro Conservation Area are about 23% and 44% grasslands, respectively

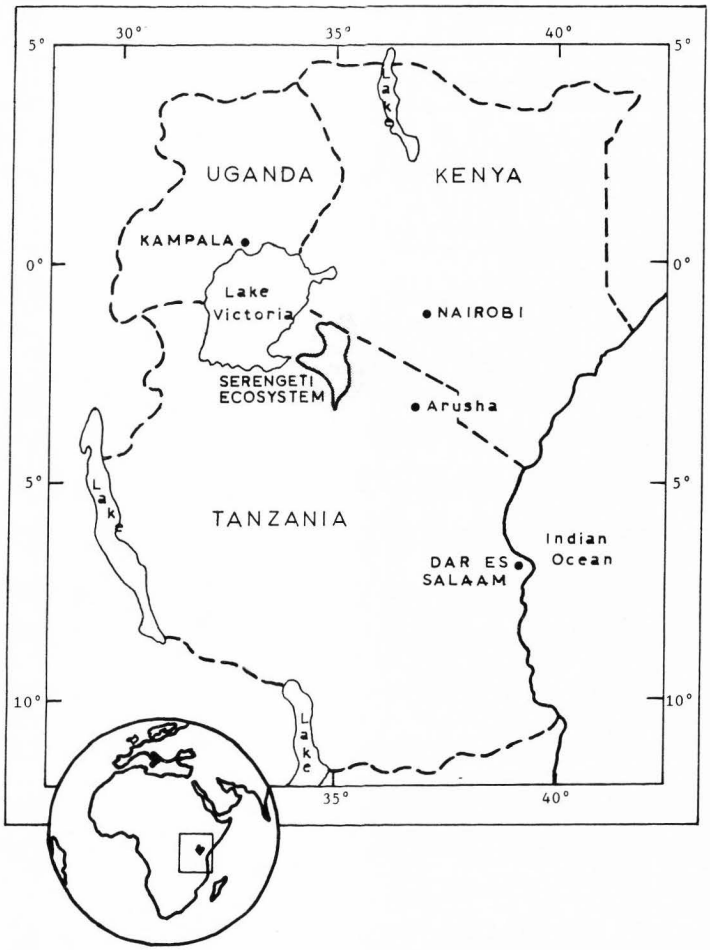


Figure 2.1 Location of the Serengeti ecosystem in Tanzania and Kenya, East Africa. The ecosystem (shaded) is defined by the ranges of the migratory ungulates. The Serengeti National Park (solid line) lies entirely within the ecosystem.

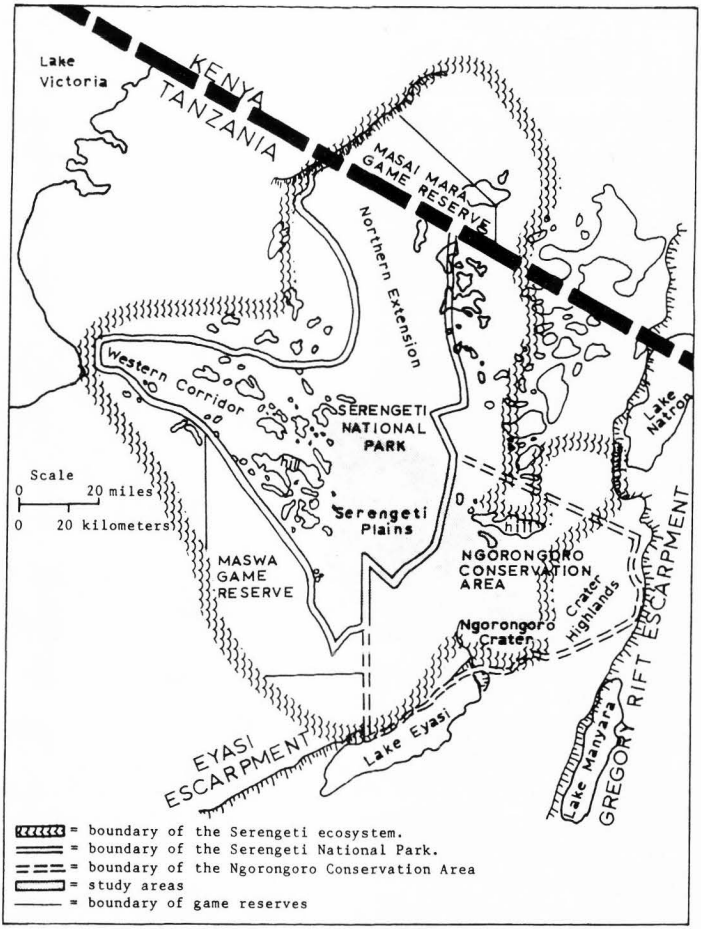


Figure 2.2 Location of the Serengeti Plains and Ngorongoro Crater in the Serengeti ecosystem of Tanzania.

(estimated from vegetation maps of Herlocker and Dirschl 1972; Herlocker 1973; and my field experience throughout the ecosystem). My two study areas--the Serengeti Plains and the Ngorongoro Crater--lie mainly within these grasslands.

Annual rainfall is nearly 1,000 mm in the northwest and southeast, with a gradient dropping to less than 400 mm at Oldupai Gorge (southeast of the ecosystem's center), because of the rain-shadow effect of the Crater Highlands. The seven-month-long rainy season, November through May, is bimodal. Rains begin in November and reach a peak in December. There is less rain from January to March, but the rain builds to a second peak in April. For the ecosystem as a whole, April is the wettest month, and July the driest (Norton-Griffiths et al. 1975). See Sinclair and Norton-Griffiths (1979) and McNaughton (1983; 1984) for a general description of the abiotic and biotic components of the Serengeti ecosystem.

2.2 The Carnivores

The Serengeti ecosystem contains 27 species in the mammalian Order Carnivora (Appendix A). However, only seven of these--the lion, spotted hyena, leopard, cheetah, African wild dog, black-backed jackal, and common jackal--are known to depend substantially upon ungulate prey. Striped hyenas feed relatively little on ungulates (Kruuk 1975a:78, 1976), and they also are rare on the Serengeti Plains and apparently absent from Ngorongoro Crater. Caracals are reported to prey on ungulates in South Africa (Grobler 1981), but there are no such records from the Serengeti ecosystem. Although male baboons often have been observed catching gazelle fawns in the Serengeti (e.g. Cullen

1969:61), gazelles represent only a small part of their diet, so they are not considered here to be carnivores.

The Carnivora rarely kill more prey than they can eat. The occasional instances of surplus killing by spotted hyenas and other carnivores was reviewed by Kruuk (1972a, 1972b, 1975a). It, however, is not important for present purposes.

Eleven ungulate-eating birds, primarily scavengers, also must be considered. These include six species of vulture--African white-backed, Rüppell's, lappet-faced, white-headed, hooded, and Egyptian--and the bateleur eagle, tawny eagle, marabou stork, white-necked raven, and black kite (Appendix B). The bateleur, tawny eagle, white-necked raven, and black kite largely eat non-ungulate foods, so carrion is only a small part of thier diet (Houston 1980). The hooded vulture, Egyptian vulture, and marabou stork obtain only part of their food from carcasses (Houston 1980). The other four vultures feed almost entirely on carrion (Houston 1980). The lammergeyer depends mainly on carrion, but is omitted because of its rarity (Houston 1980). In Ngorongoro Crater, Cape rooks were infrequent scavengers on the kills made by African wild dogs (Estes and Goddard 1967), but they are not included because I never saw them scavenge on the Serengeti Plains or in Ngorongoro Crater.

Several large carnivorous reptiles also live in the ecosystem. Pythons in the Serengeti are known to eat adult female Thomson's gazelles (M. Turner, pers. comm., cited in Schaller 1972:350) and other mammals and birds (Cullen 1969:115-118). The python seems to be rare, however, and therefore is omitted. Crocodiles occur in the rivers of the Serengeti's woodlands, and are capable of catching and eating a

half-grown zebra (Cullen 1969:110), but they are omitted because they are absent from the two study sites. Lack of information precludes consideration of blood-and-flesh-eating invertebrates, such as beetles, flies, and ants (discussed by Houston 1979), otherwise I would argue that they are important ungulate-eaters.

In my assessment the main ungulate-eaters consist of seven mammalian and eight avian species. The seven Carnivora are the lion, spotted hyena, cheetah, leopard, African wild dog, black-backed jackal, and common jackal. The eight carnivorous birds are the African white-backed vulture, Rüppell's vulture, lappet-faced vulture, white-headed vulture, hooded vulture, Egyptian vulture, tawny eagle, and marabou stork. Most, but not all, of the energy these animals require is obtained from ungulate flesh. These are the vertebrates that depend primarily on the same set of food resources.

Estimated populations of all Carnivora species in the Serengeti ecosystem are presented in Table 2.1. This apparently helps to fill a gap in the literature, for Bourliere (1983:467) claimed that no estimate had been made of the population density of an entire carnivorous and insectivorous mammalian fauna anywhere in the tropics. The densities are described in Section 6.2. The abundance of carnivorous birds is unknown. Appendix C provides more information about the Serengeti's carnivores.

2.3 The Herbivores

The prey resource upon which many of the Serengeti's Carnivora depend includes most of the 130 mammalian species reported to occur in the ecosystem (cf. Hendrichs 1972). Most of the large ungulates on the

Table 2.1 Approximate 1977 population sizes of all Carnivora in the 35,500 sq km Serengeti ecosystem. The referent year 1977 was selected because that is the year of the carnivore censuses on the plains. Also, 1977 is the year of maximum wildebeest numbers, although there was no detectable change in Thomson's gazelle numbers between 1971-78, nor in zebra numbers from 1961-1980 (Sinclair and Norton-Griffiths 1982).

Species[1]	Population Estimate	Reference
Lion	3,170	2
Spotted hyena	12,970	2
Cheetah	1,000	3
Leopard	875	4
Striped hyena	100	5
African wild dog	200	6
Cape clawless otter	100	5
African civet	700	4
Two-spotted palm civet	100	5
Black-backed jackal	24,225	2
Common jackal	12,480	2
Caracal	1,225	4
Serval	875	4
Side-striped jackal	265	4
Aardwolf	525	4
Ratel	350	4
White-tailed mongoose	3,500	4
African wild cat	4,200	4
Egyptian mongoose	1,750	4
Marsh mongoose	100	5
Bat-eared fox	13,700	2
Large-spotted genet	10,500	4
Common genet	4,900	4
Banded mongoose	35,000	4
Zorilla	2,625	4
Slender mongoose	8,225	4
Dwarf mongoose	44,625	4

1 Listed in order of decreasing body weight of adults. Their systematic relationships are shown in Appendix A.

2 Same method as for Footnote 4, except that estimates for the 8,750 sq km of grasslands in the ecosystem were added; they were

calculated from the Serengeti Research Institute (1977b) dry season transect survey and multiplied by 2.9 to represent the entire grassland area in the ecosystem.

3 G.W. Frame and L.H. Frame, in prep.

4 After Hendrichs (1970); his estimate was for an area of 15,000 sq km. There are about 26,250 sq km of bushlands and woodlands in the 35,000 sq km ecosystem, so his estimate is multiplied by 1.75. Although Hendrichs' estimates were made in 1968, they are accepted here without adjustments as being the best estimates for the 1977 populations.

5 G.W. Frame, best guess.

6 L.H. and G.W. Frame, unpubl. data.

African continent are abundant in the Serengeti. Wildebeest and African buffalos have increased phenomenally in the past several decades (Sinclair 1979). Population estimates are given in Table 2.2. An estimated 40,000,000 kg of ungulate meat is eaten by predators and scavengers in the Serengeti ecosystem each year (Houston 1979). About 30% of the total annual ungulate mortality is caused by predation. The remaining 70% provides the primary food resource upon which the vultures depend (Houston 1979). The unstriped grass mouse is the only small rodent listed in Table 2.2. As the Serengeti's most abundant rodent, it is of considerable ecological importance, because it consumes huge quantities of vegetation (Senzota 1982, 1983) and provides a reliable food for smaller Carnivora such as jackals (Moehlman 1978) and servals (Geertsema 1976, 1981).

With few exceptions the populations of non-mammalian prey will not be discussed because they are relatively unimportant to the ungulate-eating mammals and birds. Most of the non-ungulate food eaten by individuals in this guild consists of small mammals (eaten by leopards) and fruits (eaten by jackals).

2.4 Study Areas

The Serengeti ecosystem is too vast an area to study carnivores in detail, so the field research was mainly restricted to the Serengeti Plains and the Ngorongoro Crater.

2.4.a Serengeti Plains

The primary study area centers on the Serengeti Plains (Fig. 2.2) and includes about 4,200 sq km of grasslands plus 1,000 sq km of

Table 2.2 Approximate 1977 population sizes of the most conspicuous herbivorous mammals and ostrich in the 35,500 sq km Serengeti ecosystem.

Species[1]	Population Estimate	Reference
African elephant	3,850	2
Hippopotamus	500	3
Black rhinoceros	1,500	4
Giraffe	26,270	5
African buffalo	75,000	6
Eland	28,180	7
Burchell's zebra	200,000	8
Greater kudu	100	3
Roan antelope	228	2
Waterbuck	3,540	5
Blue wildebeest	1,440,000	8
Oryx	300	9
Kongoni	26,445	7
Topi	172,160	7
Lesser kudu	100	3
Warthog	33,330	10
Ostrich	5,320	11
Bush pig	100	3
Impala	221,920	5
Grant's gazelle	52,000	12
Sitatunga	100	3
Bushbuck	1,400	2
Bohor reedbuck	2,975	2
Mountain reedbuck	100	3
Thomson's gazelle	650,000	8
African porcupine	875	2
Klipspringer	1,000	3
Oribi	4,725	2
Steenbok	4,375	2
Red forest duiker	1,000	3
Common duiker	8,750	2
Suni	100	3
Kirk's dik dik	56,000	2
Hyraxes, three species	2,100,000	2
Spring hare	87,500	2
Hares, three species	200,000	13
Unstriped grass mouse	176,000,000	14

1 Listed in order of decreasing body weight of adults. Their

systematic relationships are shown in Appendix A.

2 After Hendrichs (1970); his estimate was for an area of 15,000 sq km. There are about 26,250 sq km of bushlands and woodlands in the 35,500 sq km ecosystem, so his estimate is multiplied by 1.75. Although his estimates were made in 1968, they are accepted here without adjustments as being the best estimates for the 1977 populations.

3 G.W. Frame, best guess.

4 After G.W. Frame (1980); extrapolated to 35,500 sq km ecosystem, less the settled areas.

5 After Sinclair (1972) and Grimsdell (1979); adjustments for population changes in each stratum were applied to Sinclair's total census area estimate, and the adjusted total was multiplied by 2.74 to represent the entire woodlands of the ecosystem.

6 Sinclair (1979:84).

7 Same method as for Footnote 5, except that estimates from the 8,750 sq km of grasslands in the ecosystem were added; they were calculated from the Serengeti Research Institute (1977b) dry season census and multiplied by 2.9 to represent the entire grassland area in the ecosystem.

8 Sinclair and Norton-Griffiths (1982).

9 G.W. Frame, unpubl. data.

10 Same method as for Footnote 2, except that estimates for the 8,750 sq km of grasslands in the ecosystem were added; they were calculated from the Serengeti Research Institute (1977b) dry season census and multiplied by 2.9 to represent the entire grassland area in the ecosystem.

11 After Serengeti Research Institute (1977b); the dry season density on the grasslands is extrapolated to total the number in the entire ecosystem.

12 Sinclair (1979:86).

13 G.W. Frame and F.H. Wagner (1981).

14 After Senzota (1982); from his unstriped grass mouse density estimate of 67/ha in habitats of 40% bush cover, I extrapolated to 26,250 sq km of bushlands and woodlands. For comparison, the 17 to 63 rodents/ha that were reported in the grasslands of Rwenzori National Park, Uganda (Cheeseman and Delany 1979) are extrapolated to an area the size of the Serengeti ecosystem, giving a population estimate of up to 220,000,000 rodents. The magnitude of this lends support to the unstriped grass mouse estimate for the Serengeti.

surrounding Acacia wooded grasslands (sensu D.J. Pratt et al. 1966), all of which are within the coordinates 2°27' to 3°07' south latitude and 34°41' to 35°23' east longitude. The Serengeti Plains is an old peneplain on very old crystalline rocks, and is characterized by a blanket cover of volcanic ash (Gerresheim 1974). Its elevation is mostly 1,300 to 1,450 m above sea level. Mean annual rainfall on the plains is 500 to 700 mm (Norton-Griffiths et al. 1975; L. Pennycuick and Norton-Griffiths 1976). Monthly averages of maximum daily temperatures are 25 to 32°C and minimum daily temperatures are 11 to 18°C (Kruuk 1972a:12). The hottest months are September and October, the coldest are July and August (Schaller 1972). In July and August there is a strong wind daily from the east. Soils and vegetation were described by M. Grzimek and B. Grzimek (1960), G.D. Anderson and L.M. Talbot (1965), Herlocker (1973, 1976), Schmidt (1975), Kreulen (1975), Banyikwa (1976), Sabuni (1977), deWit (1978), and McNaughton (1976, 1979a, 1979b, 1983). An overview and summary of much of the research results in the Serengeti through 1978 is provided by Lamprey (1979).

Wet-season rainfall (November to May) generally totals 400 to 550 mm on the Serengeti Plains (Maddock 1979:34). Mean monthly wet-season rainfall from 1965-76 was about 73 mm (calculated from data in Hanby and Bygott 1979:258-259). Grass production in the wet season varies from 600 to 11,500 kg/ha/season (= 60 to 1,150 g/sq m/season), and crude protein production is as high as 27% (Braun 1973). The net above-ground primary production is strongly affected by grazing intensity (McNaughton 1979a). Daily wet-season grassland production is consistently above 20 g/sq m/day, and the extreme is 40 g/sq m/day, suggesting that the Serengeti grasslands are among the most productive

in the world (McNaughton 1979b).

Mammalian use of the Serengeti Plains increases by several orders of magnitude after the rains begin (Maddock 1979). Migratory herds of wildebeest, zebras, and gazelles move from the woodlands to the open grasslands, with many carnivores following them. The wet-season populations of the large Carnivora and herbivores on the plains are listed in Tables 2.3 and 2.4.

Dry-season rainfall (June to October) generally totals 100 to 150 mm on the Serengeti Plains (Maddock 1979:35). Mean monthly dry-season rainfall was near 15 mm from 1967-71, increased to about 30 mm from 1972-76 (calculated from data in Hanby and Bygott 1979:258-259), and thereafter reverted to the earlier level (Maddock 1979:36). Grass production on the plains during the dry season is about 2 kg/ha/season (= 0.2 g/sq m/season) for each millimeter of rainfall (Braun 1973).

The Serengeti Plains desiccate quickly at the start of the dry season. With the departure of the migratory ungulates, their major predators must retreat to the drainages where pockets of prey persist throughout the dry season, or else follow the migratory herds (Tables 2.3 and 2.4). Average biomass of ungulate prey in the dry season near the center of the plains was 950 kg/sq km in 1975 and 850 kg/sq km in 1976, although in July of both years the biomass declined to a minimum of 25 kg/sq km (Hanby and Bygott 1979:257-258). The dry-season and wet-season populations of large Carnivora and herbivores on the plains are compared in Tables 2.3 and 2.4.

2.4.b Ngorongoro Crater

The Ngorongoro Crater study area comprises the floor, inner walls,

Table 2.3 Population estimates of ungulate-eating Carnivora on the 3,000 sq km central Serengeti Plains in 1977.

Species[1]	Population Estimates by Season				
	Wet-season Estimate	95% confidence Interval	Dry-season Estimate	95% confidence Interval	Reference
Lion	653	298-1,008	96	0- 200	2
Spotted hyena	3,393	2,562-4,224	852	444-1,260	2
Cheetah	251	59- 443	83	13- 153	2
Leopard	60		30		3
African wild dog	26		26		4
Black-backed jackal	488	262- 714	208	88- 328	2
Common jackal	1,843	1,170-2,516	1,286	918-1,654	2

1 Listed in order of decreasing body weight of adults. Their systematic relationships are shown in Appendix A.
2 Serengeti Research Institute (1977a, 1977b); 2,998 sq km of the central plains, corresponding to census areas 1-16 in Kruuk (1972a:47, 304-305).
3 G.W. Frame, best guess.
4 L.H. Frame et al. (1979).

Table 2.4 Population estimates of the most-conspicuous herbivores on the 3,000 sq km central Serengeti Plains in 1977.

	Population Estimates by Season					
	Wet Season			Dry Season		
Species[1]	Estimate	95% Confidence Interval	Ref.	Estimate	95% Confidence Interval	Ref.
African elephant	5		2	5		2
Black rhinoceros	65		3	30		2
Giraffe	10		2	10		2
African buffalo	200		2	20		2
Eland	200		4	100	0- 234	6
Burchell's zebra	67,000		5	0		5
Waterbuck	10		2	10		2
Blue wildebeest	480,000		5	0		5
Oryx	300		2	20		2
Kongoni	2,000		4	488	223- 753	6
Topi	4,000		4	916	275- 1,557	6
Warthog	1,873	1,237-2,509	6	1,233	814- 1,652	6
Ostrich	2,181	1,079-3,283	6	458	272- 644	6
Grant's gazelle	50,000		4	23,464	13,474-33,454	6
Bushbuck	50		2	50		2
Bohor reedbuck	200		2	200		2
Thomson's gazelle	207,000		5	44,448	29,174-59,722	6
Steenbok	500		4	500		4
Kirk's dik dik	1,000		4	1,000		4
Rock hyrax	1,000		4	1,000		4
Bush hyrax	1,000		4	1,000		4
Spring hare	10,000		4	10,000		4
Crawshay's and Cape hares	28,800		7	28,800		7
Unstriped grass mouse	600,000		4	150,000		4

1 Listed in order of decreasing body weight of adults. Their systematic relationships are shown in Appendix A.

2 G.W. Frame, unpubl. data.

3 G.W. Frame (1980); adjusted to 3,000 sq km of plains.
4 G.W. Frame, best guess.
5 Sinclair and Norton-Griffiths (1982); adjusted to 3,000 sq km of plains.
6 Serengeti Research Institute (1977a, 1977b); 2,998 sq km of the central plains, corresponding to census areas 1-16 in Kruuk (1972a:47, 304-305).
7 G.W. Frame and F.H. Wagner (1981); adjusted to 3,000 sq km of plains.

and rim of the 265 sq km caldera (coordinates 3°05' to 3°15' south latitude and 35°30' to 35°40' east longitude), about 30 km east of the Serengeti Plains. The caldera lies within the eastern boundary of the Serengeti ecosystem, but the faunal exchange with the rest of the ecosystem is somewhat restricted (Estes and Small 1981). The elevation of the floor of Ngorongoro Crater is 1,450 to 1,700 m, and the top of its rim is about 2,225 m. Mean annual rainfall at the caldera averages 908 mm on the rim, 797 mm on the north floor, and 628 mm on the west floor (G.D. Anderson and Herlocker 1973). The mean maximum temperature is about 20°C, with November being the hottest month. Mean minimum is about 4°C, in June and July (G.D. Anderson and Herlocker 1973). Soils and vegetation were described by Herlocker and Dirschl (1972), and G.D. Anderson and Herlocker (1973). Fosbrooke (1972) provided a general description of the ecology and settlement history.

Wet-season rainfall (November to May) on Ngorongoro Crater's rim averages about 829 mm, or about 118 mm per month (calculated from data in G.D. Anderson and Herlocker 1973), and is less on the caldera floor.

Ngorongoro Crater's populations of large Carnivora and herbivores are listed in Tables 2.5 and 2.6. A periodic net emigration of wildebeest and zebras (Estes and Small 1981), plus predation on all ungulates, result in a relatively stationary prey population. The density of large herbivores within the caldera is about 94 per sq km, calculated from data in Estes and Small (1981).

Dry-season rainfall (June to October) on Ngorongoro Crater's rim averages 79 mm, or about 16 mm per month (calculated from data in G.D. Anderson and Herlocker 1973), and probably is less on the caldera floor.

Table 2.5 Population estimates of all Carnivora in the 265 sq km Ngorongoro Crater in 1977. These are all the species of Carnivora that have been reported to occur within the rim of the caldera (ole Saibull 1967).

Species[1]	Population Estimates: Year-round Total	95% Confidence Interval	Reference
Lion	100		2
Spotted hyena	489	275-627	2
Cheetah	8		3
Leopard	10		3
African wild dog	0		4
Black-backed jackal	81	32-130	2
Common jackal	48	19- 77	2
Serval	20		3
Side-striped jackal	10		3
Ratel	10		3
White-tailed mongoose	40		3
African wild cat	30		3
Marsh mongoose	10		3
Bat-eared fox	109	64-154	2
Large-spotted genet	100		3
Common genet	100		3
Slender mongoose	100		3

1 Listed in order of decreasing body weight of adults. Their systematic relationships are shown in Appendix A.
2 Bygott and Hanby (1977).
3 G.W. Frame, unpubl. data.
4 African wild dogs are now only occasional in Ngorongoro Crater (L.H. and G.W. Frame, unpubl. data).

Table 2.6 Population estimates of herbivorous mammals and ostrich in the 265 sq km Ngorongoro Crater, taken as representative for 1977. These ungulate species are all the ungulates that have been reported to occur within the rim of the caldera (ole Saibull 1967). Several non-ungulate species are included because they are discussed in the text.

Species[1]	Population Estimates			
	Wet Season	Dry Season	Year-round	Reference
African elephant	32	14		2
Hippopotamus	28	23		2
Black rhinoceros	31	14		2
African buffalo	661	228		2
Eland	387	214		2
Burchell's zebra	4,026	4,499		2
Waterbuck	59	31		2
Blue wildebeest	13,764	16,535		2
Kongoni	140	145		2
Warthog			11	3
Ostrich	38	29		2
Grant's gazelle	1,599	1,578		2
Bushbuck			20	4
Bohor reedbuck			40	4
Mountain reedbuck			10	4
Thomson's gazelle	3,090	3,657		2
Klipspringer			10	4
Steenbok			10	4
Rock hyrax			10	4
Tree hyrax			10	4
Spring hare			100	4
Hare			1,000	4
Unstriped grass mouse			100,000	4

1 Listed in order of decreasing body weight of adults. Their systematic relationships are shown in Appendix A.
2 Estes and Small (1981); mean of 33 censuses and surveys.
3 G.W. Frame and J.P. Hanby, unpubl. data.
4 G.W. Frame, unpubl. data.

Ngorongoro Crater's many ungulate species concentrate around the streams and swamps on the caldera floor or retreat to the forested rim during the dry season. These movements generally are only several kilometers, keeping them within the bounds of my study area. The caldera's large herbivore populations appear to change relatively little in numbers seasonally (Table 2.6), although there is a discernable overall dry-season increase due mainly to an influx of wildebeest from far beyond the rim (Estes and Small 1981). Compared to the Serengeti Plains, the steady availability of abundant prey makes Ngorongoro Crater essentially a stable environment for the large predators.

CHAPTER III

METHODS

3.1 Field Procedures

3.1.a Study Period

Cheetah and African wild dog data were collected in the two study areas from 1972-78 by G.W. Frame and L. Herbison Frame. Also I did several months of preliminary fieldwork in 1965-66. Our fieldwork was done to gather detailed behavioral and ecological information about these two species. It was not our intention to do a comparative study of the ungulate-eaters, otherwise we would have collected data in a consistent manner for all ungulate-eaters. The descriptions and analyses in the present exercise, therefore, must draw upon data collected by many different researchers (cf. Appendix C).

Cheetahs and African wild dogs, as well as most of the other carnivores and their prey, have been studied in the Serengeti ecosystem by a succession of researchers since the 1950's (many are listed in Sinclair and Norton-Griffiths 1979:362-382). Since 1966, most of these field studies were done by scientists working through the Serengeti Wildlife Research Institute, with approval of Tanzania's National Scientific Research Council. Some of these researchers are listed in Appendix C.

3.1.b Logistics

Field procedures for studying cheetahs and African wild dogs were constrained by the rarity of these species, which could neither be found systematically nor at will. We searched by driving cross-country, stopping frequently on hill tops or other places of good visibility, to scan with binoculars. Because most cheetahs and African wild dogs are far-ranging, individuals could not be sighted with regularity. All individuals seen were photographed, described, and assigned an identification number in a file. In this way life-history data were compiled on known individuals. Some sightings were as brief as a few minutes, most were of several hours, while others were continuous throughout daylight and darkness for several days or longer. Additional details of how these two species were studied are described in G. and L. Frame (1981) and L.H. Frame et al. (1979). Other carnivores were investigated in similar ways as detailed in Appendix C.

3.1.c Sampling Methods

Several methods of data collection were employed. After an initial period of familiarization with the study animals, I prepared standardized data sheets for more consistent recording of ecological and behavioral information at each sighting. Some data were recorded continuously, some were instantaneous scan samples at 15-min intervals, and some were focal animal samples (sensu Altmann 1974) of 15-min duration, but not all of these data are used in the analyses that follow. For some types of data, verbal information was tape-recorded

and later transcribed. Biases resulting from poor visibility were compared for these different sampling methods by J.L. Wagner (1981). Beginning in 1974, all the carnivore researchers at the Serengeti Wildlife Research Institute coordinated their data-collecting methods to facilitate cross-species comparisons, but most of the results are not yet available.

The behavioral activity of individuals or each member of groups was recorded in 18 categories (Appendix D). I recorded activity observations as instantaneous samples at 15-min intervals in all quarter-hours of the 24-hr day, but with unequal sampling intensity. When poor visibility prevented seeing the activities of all of the group members, or if other work was more pressing, the sample period was skipped. Time of sunrise and sunset varies by about 20 min throughout the year, and weather conditions substantially affect the time and duration of dawn and dusk, so these data are combined into one-hour intervals to be less sensitive to these variations. Comparable data for the other carnivores were obtained from the literature.

Additional details of the Serengeti ecosystem and its flora and fauna, the study areas, and the methodology are introduced where needed throughout this paper.

The initial field research on many of the large mammals in the Serengeti ecosystem generally was of a natural history approach. The joint study of cheetahs and African wild dogs, for example, began with the question "Why are these two carnivores so rare in the seemingly ideal conditions of the Serengeti ecosystem?" As field studies of individual species progressed, patterns emerged and more specific

questions and hypotheses were formulated. Data were collected not only to address these questions, but also to provide general ecological and behavioral descriptions.

The value of this initially broad approach in ecological research was discussed by McNaughton (1977), Westoby (1981), Humphreys (1981), and May (1981). Advocates for the use of the hypothetico-decuctive method as a means of developing a better understanding of the patterns and processes involved in community structure are Colwell and Fuentes (1975), Connell (1975), and Romesburg (1981). All, however, probably would agree that there is value and necessity in employing both approaches.

Data that were collected for other purposes, and then used to test a hypothesis, are more likely to be free of observer-expectancy bias than are observations that are made specifically to test a particular hypothesis (D.F. Balph and M.H. Balph 1983). The present study uses data ex post facto to test hypotheses and conceptual models that were formulated by other researchers for other ecosystems.

3.2 Niche Descriptions

Competition usually is difficult to identify and evaluate in natural systems because of the complexity and lack of experimental control. The task is even harder in national parks and nature reserves because the researchers may neither desire, nor be permitted, to manipulate the study animals or the resources to achieve population responses. How then can competition be assessed?

In the present study, much of the evidence for competition among carnivores in the Serengeti ecosystem is circumstantial. The scene

is set by examining similarities in resource use among the large Carnivora and vultures by examining their niches. Then prey and predator densities and ratios are calculated to identify likely times or places of prey shortages. This leads to describing seasonal and locational niches to see how resource-use similarities change. Then the evidence for competitive exclusion and interference competition are described. Several models of niche dynamics in a competitive community are tested to see if they are descriptive of the Serengeti's carnivores. The Serengeti carnivore community has existed for a very long time, so carnivore body sizes are tested for evidence of character displacement. The methodology of these approaches is described as follows, beginning with the niche descriptions:

The niche, with its several measures of comparison, is a common model of resource use by organisms. The two most commonly used descriptors are niche breadth and overlap, although cluster analysis and graphical presentations provide additional information. Sometimes a one-dimensional niche description is adequate for showing ecological or behavioral similarities in resource use among organisms, and the abstraction of greatest interest or importance usually is the food resource. Often, however, a multidimensional niche is more informative. The definition and measurement of niches have been refined by several authors to provide a more precise and useful understanding of relations among species (Hutchinson 1957, 1978), among divisions within species such as sex and age classes or social groupings (Roughgarden 1972; Wiens 1974, 1977:593; Hutchinson 1978; Clutton-Brock et al. 1982), and even among individuals (MacMahon et al. 1981).

The description of a single niche, whether it is that of an individual organism, an intraspecific sex, age, or social class, or an entire species seldom is of interest in itself. The utility comes in comparing niches. Although two species can be shown not to occupy the same niche, it is never possible to show that they do occupy the same niche (MacArthur 1968). In fact, by definition, every organism has a unique niche (MacMahon et al. 1981). In the three-toed sloth, for example, food niches differ among individuals of the same sex (Sunquist 1986). To illustrate some of these niche differences, the various carnivores living in the Serengeti ecosystem are arranged along resource axes to show their use of foods, habitats, and other resources.

Ecological relationships among the Serengeti carnivores are described by measures of niche breadth and niche overlap, by graphical representations of their niches, and by cluster analyses. These are methods of illustrating the degree of ecological similarity among organisms, and perhaps the potential for competition, but they are equivocal measures or evidence of competition. The purpose of comparing niches is to provide informative descriptions of the ungulate-eating guild and the carnivore community (sensu MacMahon et al. 1978) and to evaluate whether or not these kinds of analyses are adequate techniques for identifying the types and intensities of competition actually observed (Sections 10.1 and 10.2).

First, generalized year-round niches are described (Chapters Four and Five). All the Carnivora species living in the Serengeti ecosystem (Table 2.1) are arrayed along resource axes. Unidimensional niches show the extent of niche separation and overlap along what generally is

considered to be the most important single resource axis for mammals and birds. This is expected to demonstrate clumpings around several food sizes, for example. One aggregation would be the ungulate-eaters. The ungulate-eating predators and scavengers are examined in more detail by considering their niches. Cheetahs are examined in particular detail by considering intraspecific year-round multidimensional niches.

Second, niche changes that result from seasonal variations in resource availability are described (Chapter Seven). For the Serengeti Plains data, multidimensional niches of the ungulate-eaters in the wet season (November to May) and in the dry season (June to October) are compared. This requires compiling two resource matrices, one for each season. The niche of an organism varies as the organism responds to changes in resource availability, interacts with competitors and predators, or undergoes motivational or physical changes. Thus, seasonal comparisons should be enlightening. Vandermeer (1972) discussed the dynamic nature of niches.

Third, niche differences that occur in different areas of the ecosystem are described (Chapter Eight). Niches of the ungulate-eaters in the variable environment of the Serengeti Plains is contrasted with the relatively stable environment of Ngorongoro Crater. The latter is essentially stable from the carnivores' point of view because a permanent supply of water and forage allows most of the herbivores to remain there throughout the year. Thus, the carnivores have an unvarying supply of food, water, and cover. The resource-use data for the large carnivores are presented in two resource matrices, one comprising species during all seasons in Ngorongoro Crater.

Within-species niches are also described for the cheetah. Five niches based on sex, age, and social groupings are compared (Chapter Eleven).

3.2.a Resources Measured

A niche hypervolume in multidimensional space (sensu Hutchinson 1978) is difficult to measure because of the large number of possible axes. Even if a niche could be adequately described, the number of axes might be so numerous that the data would become difficult to interpret (Maguire 1967; R.H. Green 1971:543-544). There also is a serious problem of deciding what constitutes a meaningful resource axis (Soule' and Stewart 1970). No matter how many resources are measured, the inclusion of one more resource might significantly alter the niche hypervolume. Significant similarities can be created or eliminated by using different axes. Resources considered to be most important by the researcher might not be most important to the organism being studied.

Some problems complicating niche comparisons have been overcome by considering only those axes which separate organisms and along which organisms are serially arranged (Cody 1974:52). It is the differences which are important, so the many axes which are redundant, irrelevant, or invariant are deleted (Hutchinson 1978). Other researchers have used discriminant function analysis (Hope 1968) as a means of deciding which of the measured niche axes probably are most important. Significant discrimination among groups assumes a linear relationship. A study of molluscs (R.H. Green 1971) used this method to good effect. Also, in a study of African ungulates (Ferrar and Walker 1974), three

of the 20 measured variables were found to account for 65% of the among-species variance. For the Serengeti data, however, I designate the most important axes for the one-dimensional niches as those where the observed actual competition and surmised potential competition are concentrated. For the multidimensional niches, all the measured axes are included.

In this study, the problem of describing niche axes was addressed by measuring the resources which were most conspicuous as well as those which were expected to be most important. All resources used in these analyses were selected because they seem to be biologically meaningful, either directly or indirectly. This decision in turn determines the degree to which the analyses accurately describe the organisms. Some resources are correlated with each other, however, even though in the multidimensional niche the orthogonality of the resource axes implies that they have no correlation (Hutchinson 1978).

The way a human defines what constitutes a resource continuum, might be very different from the way another organism perceives it (Soule' and Stewart 1970). The use of high taxonomic levels of prey identification such as species or genus, rather than prey size, is recommended for the calculation of niche breadth, because lower levels consistently give smaller estimates (Greene and Jaksic' 1983). Some other important variables in niche descriptions are location (Hutto 1981), time (Carothers and Jaksic' 1984), and temperature (Bernstein 1979), although Tilman (1982) maintains that temperature is not a resource. Tilman (1982) defines a resource as a substance or factor, consumed by an organism, that increases growth rates when its availability is increased.

Investigations of Carnivora niches are few, notable exceptions being the studies of mink (Mustela vison) and otter (Lutra lutra) in Europe (Erlinge 1972; Wise et al. 1981). Large animals are believed to have a generally greater capacity for adjustment than small animals (Emlen 1975). Organisms that possess higher degrees of learning ability should have additional degrees of niche plasticity unseen in other animals. This approach to examine niche dynamics, coupled with the quantification of simple interactions (Vernon 1970), contributes to making complex communities more understandable.

Depending upon the analysis, anywhere from 1 to 11 resource axes are used; each axis contains two or more resource states (sensu Colwell and Futuyma 1971), which are the same as attributes (sensu Romesburg 1984). These are described by physical, ecological, and behavioral data. Available data are most complete for cheetahs and African wild dogs. Analysis of the ungulate-eater guild requires deletion of some axes because of inadequate information about some species. In other analyses, poorly sampled carnivore species are deleted from the comparison, so that more resource axes can be compared for the remaining species.

Data for these axes are arranged in matrices, each of which is called a resource matrix (sensu Colwell and Futuyma 1971:567-568). Resource-use data from the several years of fieldwork are sometimes combined to form larger data sets for the analyses, a procedure studied and found acceptable as representative of a typical year (Landres and MacMahon 1983). Thus, the wet season and dry season comparison uses data from several years. Cell entries in the resource matrix are the number of observations in which a species was seen in a particular

resource state. Any resource state in which no species was recorded is deleted from the matrix (cf. Inger and Colwell 1977:233).

Using data we collected on hunting behavior and ecology of cheetahs and African wild dogs as an example, I describe nine axes and their subdivisions as follows:

(1) Diel activities. The activities of cheetahs and African wild dogs were recorded at 15-min intervals throughout the day and night. These detailed data are used to compare sexes and groups within the two species, and then compared with published data for other carnivorous species. Time is a resource which can be used in many ways. The amount of time that an individual animal or social group spends in any particular kind of activity, however, varies according to individual or group needs and in response to other organisms. The latter might be thought of as a response to interference competition from conspecifics and from other taxa.

Although Jaksic' (1982) discussed the inadequacy of activity time as a niche difference, Carothers and Jaksic' (1984) concluded that where interference competition occurs, time is a niche axis along which organisms can reduce agonistic interactions. The mutually exclusive and exhaustive categories of activity are listed in Appendix D. Of these categories, the one most likely to be a meaningful niche axis is the hour of the day when the most active hunting and eating occurred. This is an important axis because shifts in diel activities can decrease interference competition (Jaksic' 1982).

(2) Weather. This axis contains three discrete categories, namely rain, cloudy, and sunny or clear. Weather probably affects when an animal hunts, or at least when it is likely to be active. It can be

thought of as a resource-use index in that various weather types allow organisms to engage in certain kinds of activities but not in others. For example, a predator might be unable to hunt in the rain, so the availability of non-rainy weather might be a limiting resource.

(3) Vegetation types. The categories used are consistent with the terminology of D.J. Pratt et al. (1966) for East African rangelands. The following vegetation types seem to be meaningful as cover for the mammalian carnivores: Short grassland (less than 50 cm tall), medium grassland (50 to 150 cm tall), bushed grassland or wooded grassland, riverine and kopjes. The habitat type determines where an animal hunts.

(4) Prey density. The abundance of prey in a circular area with a radius of approximately 1 km from any observed cheetah or African wild dog was estimated. The density was rated on a scale of 0 to 4, originated by G.B. Schaller and B.C.R. Bertram (pers. comm.). Similar data are available for other large Carnivora. The density categories are: 0 = none, 1 = very few and widely scattered (1 to 10 prey animals), and 4 = very abundant and full migrations (>1,000 prey animals). This scale includes both the migratory and non-migratory ungulates, and, as a density index, combines all species of prey.

(5) Prey species hunted. There is some evidence that predators prefer the taste of meat of certain species (Cott and Benson 1970, cited in Thomas 1983). In calculating niche metrics, the degree of niche overlap varies according to the taxonomic levels of prey identification that are used, with species and generic data giving smaller overlap values than are given by ordinal data (Greene and Jaksic' 1983).

(6) Prey body size hunted. Of major importance to any predator is the ease, safety, and probability of success with which it can catch and kill its prey. Sex, age, and social behavior (e.g. territorial versus non-territorial) are indirect measures of the prey's body weight, alertness, and ability to escape or defend itself. The prey categories used here are defined using the criteria of other researchers who studied the individual prey species.

(7) Prey group size hunted. Prey social organization affects the vulnerability of some prey individuals within each species. Animals living alone, or in small groups, might be more vulnerable than those in large herds. On this axis, 1 represents an individual (often territorial), and all other social groupings of the prey are represented only by their group size.

(8) Hunting technique. Three discrete food-getting techniques are used as a niche axis. These are: hunting by stalking, hunting without stalking, and scavenging instead of hunting.

(9) Length of chase. This is a continuum, ranging from ambush to a lengthy chase. For convenience, it is divided into distance categories, which are: 0-10 m, 11-100, 101-300, 301-500, 501-1,000, and 1,001 or more.

I recognize the problem of sampling biases. The searching methods described in Section 3.1 give good coverage of the entire study areas. Many potential resource states were sampled on all the described niche axes. Nevertheless, some unevenness in sampling intensity does exist. For example, I sampled less in darkness than in daylight. Areas of rocks and thickets were sampled less intensely than were areas where vehicles could go. Nevertheless, only the cheetahs and African wild

dogs were sampled with the intention of describing their niches. The decision to compare all the ungulate-eaters was made ex post facto, and therefore must rely upon data from many different sources.

Despite these problems in the data, I believe that it is better to make this crude comparison of resource use among African carnivores than to do nothing at all. The problems that become apparent from these analyses should serve to show future directions for research in the Serengeti ecosystem.

3.2.b Cluster Analyses

Cluster analysis is used to identify the carnivore species and the cheetah groups that are most similar in their use of resources. The analysis is used here only when four or more objects (species or group types) are being compared.

Attributes, or resource states, considered in the cluster analyses are the same as those used in the resource matrices for computing niche breadths and overlaps and for drawing graphs (see below).

The similarity coefficient is the correlation coefficient r_{jk}, also known as the Pearson product moment correlation coefficient. The r_{jk} coefficient is insensitive to both additive and proportional translations, and therefore is used without standardizing the data matrix. Unequal sample sizes among species or group-types are compensated for by using this coefficient (cf. Romesburg 1984:101, 106-107).

The clustering method is the unweighted pair-group method, using arithmetic averages, more commonly called UPGMA (cf. Romesburg 1984). The CLUSTAR computer program (Romesburg and Marshall 1984) is used for

these analyses. Output from each data set consists of a resemblance matrix, dendrogram, and cophenetic correlation coefficient (Romesburg 1984:14-27). The cophenetic correlation shows how good the agreement is between the resemblance matrix and the dendrogram. When the cophenetic correlation coefficient, which measures the distortion in going from the resemblance matrix to the tree drawing, is 0.8 or larger, the dendrogram generally is considered to be acceptable (Romesburg 1984:26-27).

In the examples where data sets containing more than one resource axis are subjected to cluster analysis, the data are entered as marginal totals from the data matrix of each axis. This short-hand approach results in a loss of information from the original multidimensional condition (James Haefner, pers. comm.). Thus, there is doubt about how well my multi-axis cluster results represent the original multidimensional data.

My reasoning in doing the cluster analysis of multi-axis data sets by using only marginal totals is simply to compare how similar the species or groups (as abstract entities in themselves) are in their use of the resource states in several major categories such as food types, habitats, and times of day. For that question, it does not matter, for example, whether a wildebeest was eaten on short grass or in bushland, nor does it matter if it was eaten in the morning or the evening. What does matter in answering this particular question, was that the carnivore species (not the individuals) are compared by the frequency with which they ate wildebeest as opposed to other prey species, the frequency with which they used the grassland as opposed to other habitat types, and the frequency with which they ate in the morning as

opposed to the evening. Using marginal totals rather than the original multivariate data results in a loss of information, and the disparity of dendrograms done in both ways is unknown. Where marginal totals are used, therefore, the dendrogram caption so indicates, and the reader may want to be wary.

3.2.c Niche Breadths and Overlaps

Niche breadth and niche overlap are computed using the method described by Colwell and Futuyma (1971) and Colwell (1977). This method has been popular among ecologists, and is often cited, although seldom used (cf. Colwell 1982).

Niche overlap indices were criticized by Hurlbert (1978) as being inadequate, because they lack simple biological interpretations and they do not take into account the variations in abundance or availability of resource states. He proposed using indices that are interpretable in terms of encounters, based on the "mean crowding" approach described by Lloyd (1967). In the data from the Serengeti ecosystem that I used here, I am unable to quantify the availability of most resource states, primarily because of their unpredictability and patchiness. Also, there is considerable uncertainty about what constitutes "availability" to carnivores in a dynamic environment. In the present treatment, therefore, I prefer to follow the methodology described by Colwell and Futuyma (1971).

For the niche breadth and overlap calculations, data are cast into resource matrices which have carnivore species or cheetah group types as columns and resource states as rows (modified from Colwell's original program). As described in Section 3.2.a, each cell contains

the number of observations in which the carnivore was recorded as associating with the resource state. Resource states in which no carnivore was recorded are deleted from the matrix. When more than one resource axis is included in an analysis, the marginal total of the resource states on each axis is used. All unoccupied cells (resource states) are deleted from this multidimensional data matrix. The number of occupied resource states increases with the time spent observing. The sample sizes are large, however, and the absence of a species from a resource state is accepted as reflecting its real absence.

The problems of range, spacing, and non-linearity of the resource data were discussed by Colwell and Futuyma (1971). Differences in range *per se* do not affect proportional measures of niche overlap if the entire niche of each species is sampled. Colwell and Futuyma explained that spacing affects the estimates of niche overlap; there is a general tendency toward the underestimation of niche overlap from abundance data due to the abruptness or inaccessibility of ecotonal areas. Nonlinearity should not be ignored, as there is ample evidence in human psychometrics and in the response curves of physiological ecology that this is a necessary consideration. Colwell and Futuyma proposed using weighting factors based on the distribution of all the species among all the resource states. They termed this an "eco-assay" because it provides a measure of the ecological distinctness of the resource states (Colwell and Futuyma 1971; Inger and Colwell 1977). However, the eco-assay does not allow for the actual production of the resources in the environment. Hanski (1978) offered a new factor to correct for this, but it cannot be used here because of the patchy and unpredictable distribution of most of the measured resources in the

Serengeti ecosystem.

Weighting factors can be applied to the calculations of niche breadth and niche overlap in the alternative manner described by Clarke (1977:281). The abundance of each species in each habitat is represented by a ratio of the absolute abundance to the weighted mean abundance of that species in all habitats. This leads to expressing the Shannon-Wiener formula in the form of an antilog. The advantage of this approach over that of Colwell and Futuyma (1971) is that the weighted niche breadth does not depend on the value of an arbitrary constant k. Colwell (1977) agreed that this is an improvement, and provided this option in his computer program.

Niche breadth for each species is the proportion of all the weighted resource states that is used by a species. It is the inverse of ecological specialization (Colwell and Futuyma 1971). For ecological comparisons, the niche measure of Feinsinger et al. (1981) is better, but it can be used only if the relative frequencies of the available resources are known. In the Colwell and Futuyma (1971) method, it is not necessary to know the resource abundances that are available to the organisms of interest.

Niche overlap among species is calculated by comparing the distribution of individuals in all pairwise species combinations among all the resource states in the resource matrix. Comparisons of several common indices of niche overlap showed that each is dependent upon questionable assumptions (R.V. Alatalo and R.H. Alatalo 1979), leading to the conclusion that Schoener's (1970) index is most accurate (Linton et al. 1981). This index, however, has potential difficulties which prompted modification by Colwell and Futuyma (1971). That modification

was recommended as being the most accurate index, particularly for comparing communities (Landres and MacMahon 1983). The measure of proportional overlap (Colwell and Futuyma 1971:568, after Schoener 1968) will be used here. Expressed as a percentage, the overlap is a measure of ecological similarity (Schoener 1970).

The FORTRAN program for the Colwell and Futuyma (1971) method, with Clarke's modification, is used in this study. Permission to use the program was granted by R.K. Colwell (pers. comm.). The program was provided on punch cards by P. Landres, and adapted with the assistance of E. Zurcher for use on the VAX computing facilities at Utah State University.

The options to the program are described in Colwell (1977). The following options are used for comparing more than three species or groups: Natural weighting for the species or group, non-circular niche breadths, non-circular niche overlaps, relative measures, and Clarke's W'. When only two or three species or groups are compared, the computer program requires the computation of circular niche breadths and overlaps instead of non-circular. Whenever the circular option is used, it is stated so in the result. Natural weighting for the species means that each resource state is weighted in proportion to the occurrence of all species in that state, compared to the occurrence of all species in all states; this is the eco-assay described above. The non-circular method requires exclusion of the species for which the resource-state weighting factor is being computed (Colwell and Futuyma 1971; Colwell 1977). Relative measures scale the range of data from 0 to 1, rather than using the full range of the observed values. Clarke's W' employs a monotonic transformation to obtain a measure of

niche breadth (Clarke 1977; Colwell 1977), which avoids the need for arbitrarily assigning a constant, as was proposed by Colwell and Futuyma (1971).

When data sets comprise more than one niche axis, the niche breadths and overlaps are calculated separately for each axis using the Colwell niche program. Then, the multidimensional niches are calculated in three ways. This redundant approach is necessary, because the data are unavailable in the original multidimensional form. First, the product method is used, in which all the one-axis niche breadths or niche overlaps are multiplied by each other, to estimate the multidimensional breadth or overlap (cf. Hanski 1978). Second, the summation method is used, in which all the one-axis niche breadths or niche overlaps are averaged, to estimate the multidimensional breadth or overlap (cf. Hanski 1978). Third, the resource states of all the axes are run simultaneously in the niche program, although these data represent projections on to the niche axes rather than the original multidimensional condition (cf. May 1975; Hanski 1978). The results of these three different methods then are compared to obtain a general consensus of multidimensional niche relationships among the organisms of interest.

The product and summation methods are based on different assumptions. The product measure is appropriate if the niche axes are independent of each other, and the summation measure is appropriate if the axes are totally dependent (May 1975). As May pointed out, however, in nature the situation is likely to be intermediate to these two extreme conditions. Hanski (1978) showed that for his organisms, the summation measure gives a good approximation of multidimensional

niche width, and the product measure gives a good approximation of multidimensional niche overlap. An estimate of the upper limit of the multidimensional niche overlap is provided by the summation measure (May 1975).

The statistical problems associated with measures of niche breadth and overlap were discussed by Petraitis (1979), Ricklefs and Lau (1980), Linton et al. (1981), Maurer (1982), E.P. Smith (1982), Smith and Zaret (1982), and Mueller and Altenberg (1985). Because of the uncertainty of how representative some of the data sets are, no attempt is made here to calculate variances, confidence intervals, or other statistics for the niche metric results. With this limitation, the prudent course is to place minimal emphasis on the interpretation and significance of the niche breadth and niche overlap numbers. Instead consider only the most extreme similarities or differences. Generalized niche relationships should be evaluated in balance with the results of the cluster analyses and the interpretations of histograms.

The same data sets are used in both the cluster analyses and the niche metrics calculations. The computational techniques are sufficiently different that some inconsistencies are expected in the identification of the most-similar species pairs. The data are, therefore, examined graphically (see below) to try to resolve the anticipated discrepancies.

3.2.d Graphs

Graphical representations are used to show similarities in resource use among the carnivores. Chi-square tests are used for convenience throughout the niche-description chapters, although the Fisher exact

probability test (Siegel 1956:96-104) and the G test (Sokal and Rohlf 1969) are appropriate for further, more detailed analyses. A separate chi-square test for k independent samples is used on the count data of the occupied resource states on each of the niche axes. These tests show which of the resource axes have statistically significant differences in use by the carnivores.

When finely subdivided axes contain small sample sizes, the resource states are combined into fewer categories prior to testing. The most-similar resource states are combined further, so that in the r by k contingency tables fewer than 20% of the cells contain an expected frequency less than five, and no cell contains an expected frequency less than one. These criteria must be met for the results of the chi-square goodness-of-fit test to be meaningful (Siegel 1956:110, 178-179). When combining resource states fails to meet the test criteria of minimum expected cell frequencies, the carnivore species with inadequate sample sizes are deleted.

Multiple testing increases the risk of a type II error, so null hypotheses are rejected only at or below the $p = 0.01$ level. If the null hypothesis of no differences is rejected, the alternative hypothesis that some non-random differences exist is accepted. Only the axes that show a statistically significant difference in resource use by the various carnivores are used in constructing graphs.

In three-dimensional graphs, the Euclidean distance between any pair of niche centers is inversely proportional to niche overlap between those two species. The resource-states data used in these graphs are the same as those used in the cluster analyses and niche

metrics. But unlike those methods, however, the axes that fail to show a statistically significant difference are not graphed.

The results of these niche descriptions by clustering, calculating niche metrics, and graphing are compared in later chapters to the observed interference competition and to several ecological models of competition and coexistence.

3.3 Prey and Predator Densities and Ratios

The densities of prey and predators are estimated for the entire Serengeti ecosystem and the two study areas (Section 6.2). From these, the ratios of prey to predators are calculated (Section 6.3). Densities and ratios are useful for making comparisons within the ecosystem by season and by location, as well as to other areas in Africa, for evidence of resource limitations.

No attempt is made to calculate biomasses, because representative weights are not available for many of the species. At least some of the Carnivora, e.g. leopards (Jeannette Hanby, pers. comm.) and African wild dogs (Estes and Goddard 1967), appear to be smaller in the Serengeti, so weights cannot be used from elsewhere in Africa.

3.4 Competitive Exclusion

The literature is reviewed to assemble evidence of possible instances of competitive exclusion in the Serengeti ecosystem. These examples are discussed (Chapter Nine) in the context of the information presented in the earlier chapters.

3.5 Review of Carnivore Interactions

A review of published and unpublished anecdotal information about the Serengeti carnivores provides numerous examples of aggressive interactions. These constitute evidence of competition, because the teiology of aggression is always competition for scarce resources (Marler 1976). The fact that so many instances of interspecific and intraspecific aggression and killing have been observed in the Serengeti suggests that these must be common phenomena (Chapter Ten).

In other field studies (cf. Schoener 1982), interference competition often was the only form of competition detectable. It sometimes was considered to be more important than exploitation competition.

If interactions are indeed frequent or severe, their significance extends beyond the individuals involved; they are likely to result in population numerical responses. The total effect of interference interactions involving a particular individual is likely to be a change in that individual's reproductive success. And the sum effect of interference interactions involving a particular species is likely to be a change in the size or structure of the population. In either case, identifying frequent and intense interference interactions establishes the existence of competition on either one or both levels.

3.6 Community Models

Several community assembly rules are tested in Chapter Twelve. They were selected because they provide sensible explanations of how

similar species coexist, and they appear to be testable with the Serengeti data. The randomization test (B.F. Green 1977) is used. Because of multiple testing (cf. Section 3.2.d) the acceptable p-value is specified as 0.01. Data for these tests will be extracted from those used in the cluster analyses, niche metrics, and graphs.

3.7 Character Displacement

Although shifts in morphological features are of a different time scale from other competitive effects discussed here, statistical tests are used to see if the Serengeti carnivorous mammals and birds support the predicted linear and geometric size ratios. The tests of Poole et al. (1979). are used, with an acceptable p-value of 0.01 or less (Chapter Thirteen). There seems to be considerable variability in the body sizes of large Carnivora in different areas of Africa, suggesting the possibility that competition or other ecological factors might be responsible.

CHAPTER IV

INTERSPECIFIC YEAR-ROUND NICHES OF CARNIVORA

4.1 Similarity Suggests Competition

My working hypothesis is that the Carnivora species pairs that have a high degree of similarity in their use of important resources, are the ones most likely to compete at least occasionally. The purpose of this chapter, therefore, is to identify which Carnivora species are most similar in their resource use.

The generalized year-round niche relationships of the ungulate-eating Carnivora and vultures are described as a means of elucidating which carnivorous species are most similar. Although the most-similar species pairs are most likely to compete, a large niche overlap in itself is not evidence of competition. Two organisms can be very similar in their use of resources and essentially not compete, if the resources are abundantly available to them (Klomp 1961). I consider that two individuals or two species with highly similar niches--recognizable as large coefficients of resemblance, large pairwise niche overlaps, and close graphical similarity--should be thought of as being the likely foci of exploitation competition.

Eight comparisons of the year-round niches of the Serengeti ecosystem's larger Carnivora are examined in this chapter. These vary from the consideration of nine Carnivora simultaneously along one resource axis to comparisons of fewer species along one or more

resource axes. The carnivore combinations that are compared are selected because data on them were collected in similar ways and comparisons are ecologically meaningful. The resource-use data come from my own field research, carried out between 1972 and 1978, and from published and unpublished sources (Appendix C). Resource states (defined in Section 3.2.a), the frequencies with which they were observed, and references for them are listed in the Appendices.

4.2 Nine Carnivora

Five ungulate-eating Carnivora (lion, spotted hyena, cheetah, black-backed jackal, common jackal) and four additional Carnivora species (side-striped jackal, aardwolf, ratel, and bat-eared fox) are compared along one niche axis using the combined results of two transect surveys conducted in 1977 (Serengeti Research Institute 1977a, 1977b). Each survey comprised 39 transects on the Serengeti Plains (Fig. 4.1). Observers drove along transects and counted all carnivores (and a few other selected species) that were seen within 100 m on either side of the vehicle. Transect lengths varied from 4 to 66 km (mean = 27.8 km). The number of transects in which at least one carnivore was seen is 72 (out of a possible 78 in the two censuses combined; cf. Appendix E). A total of 700 carnivores was recorded. No leopards or African wild dogs were seen during the survey. The absence of leopards must be due to their avoidance of the grasslands, because this species is common within the ecosystem (cf. Table 2.1) and they are no shyer than many other Carnivora. African wild dogs, however, probably were unrecorded because of their rarity.

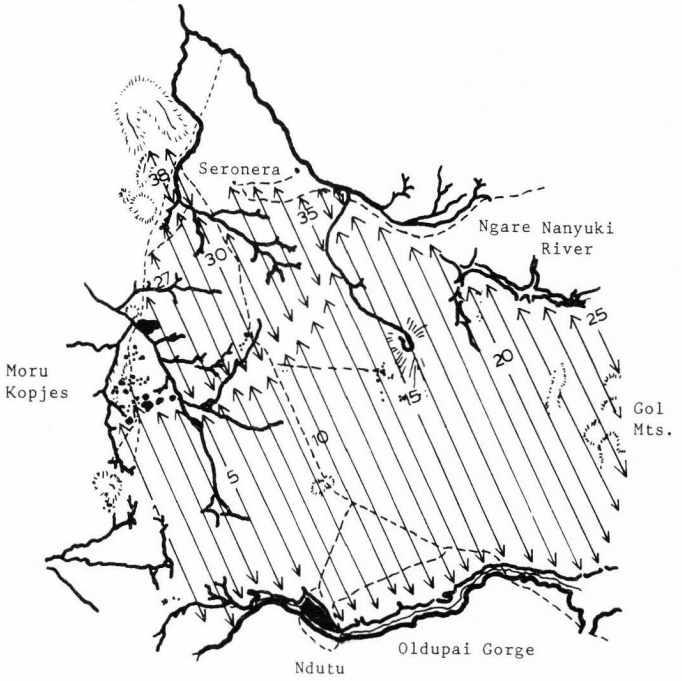


Figure 4.1 Location of 39 survey transects for wet- and dry-season counts of Carnivora on the Serengeti Plains. Redrawn from Serengeti Research Institute (1977a).

This one-axis niche analysis differs from most subsequent analyses by not directly using food, habitat, and other important single measures as the niche axes. Instead, each survey transect is used as a resource state that represents a combination of variables such as prey availability, rainfall, habitat type, and whatever else is important in influencing whether or not the Carnivora are there. Data from both surveys are combined without regard to season.

In calculating the niche metrics and cluster analysis, each of the 72 occupied transects is considered a separate resource state. But the graphical comparison combines transects and considers only three survey blocks. The 39 transects of each survey were distributed among three sampling blocks (Fig. 4.1) as follows:

I = transects 1-18, mostly a mosaic of short grasslands with Indigofera basiflora and Justicia elliotii small woody shrubs or Hypoestes herb, area = 1,778 sq km;

II = transects 19-25, mostly a mosaic of short grasslands with Hypoestes and Solanum herbs, area = 537 sq km;

III = transects 26-39, mostly medium grasslands or wooded medium grasslands with Acacia trees, area = 683 sq km.

Block II is driest of the three, and Block III is wettest. Although comparison does little to identify the important variables, it does give information about relative specialization and the degree of similar year-round resource use among the Carnivora on the Serengeti Plains.

Through cluster analysis, comparison of the nine Carnivora showed (Fig. 4.2) that black-backed jackals and bat-eared foxes are most similar in their occurrence among the 72 survey transects, i.e. these

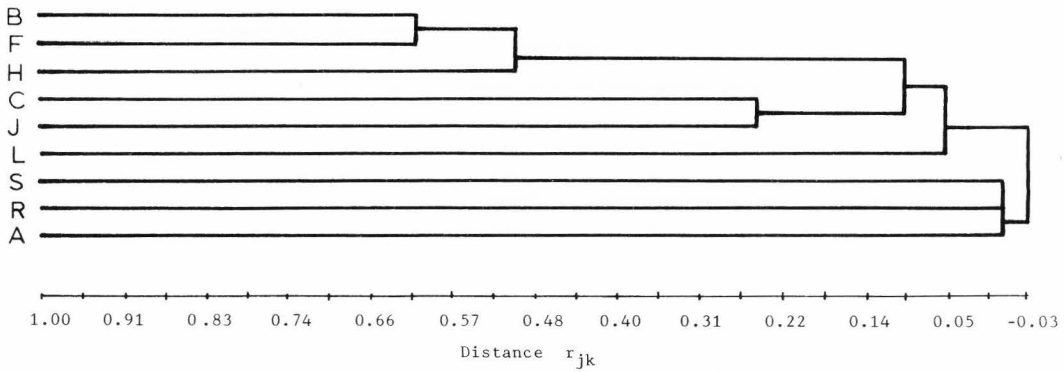


Figure 4.2 Dendrogram of nine Carnivora, showing similarity in year-round use of 72 transect locations on the Serengeti Plains. Abbreviations: L = lion, H = spotted hyena, C = cheetah, B = black-backed jackal, J = common jackal, S = side-striped jackal, A = aardwolf, R = ratel, F = bat-eared fox. Data are from Appendix E.

two species tend to be seen in the same ecological settings. The spotted hyena is the next most-similar predator. The resemblance matrix and cophenetic correlation are in Table I.1 (Appendix I).

Non-circular niche metrics (Table 4.1) show that spotted hyenas have the greatest niche breadth, which means that they are the most widely distributed Carnivora among the transect locations on the Serengeti Plains. Spotted hyenas and common jackals are most similar in their occurrence among the 72 survey transects, as measured by their high niche overlap. The side-striped jackal, ratel, and aardwolf have very small niche breadths and overlaps because of their rare occurrence in the sample transects. Side-striped jackals are virtually absent from the plains. Ratels and aardwolves actually are common on the plains, but they escaped detection because they are primarily nocturnal.

The three survey blocks, rather than the individual transects, are compared graphically in Figure 4.3. Spotted hyenas and common jackals stand apart from the other carnivores by being disproportionately abundant in survey Block I, the area that has the most shrub cover. The differences in frequency of occurrence of the six most-numerous Carnivora--lion, spotted hyena, cheetah, black-backed jackal, common jackal, and bat-eared fox--among the three survey blocks on the Serengeti Plains is statistically significant ($X^2 = 123.65$, df = 10, $p < 0.001$, two-tailed).

4.3 Seven Carnivora

All seven of the ungulate-eating Carnivora (lion, spotted hyena, cheetah, leopard, African wild dog, black-backed jackal, and common

Table 4.1 Niche breadths and niche overlaps year-round among nine Carnivora. Calculated from their occurrence in 72 survey transects on the Serengeti Plains. Abbreviations: H = spotted hyena, C = cheetah, B = black-backed jackal, J = common jackal, S = side-striped jackal, A = aardwolf, R = ratel, F = bat-eared fox.

		Pairwise Niche Overlaps							
Carnivora Species	Niche Breadths	H	C	B	J	S	A	R	F
Lion	.23	.49	.10	.47	.38	.00	.00	.00	.45
Spotted hyena	.48		.31	.68	.76	.02	.00	.00	.52
Cheetah	.15			.34	.43	.00	.00	.00	.05
Black-backed jackal	.37				.48	.00	.00	.01	.70
Common jackal	.41					.03	.01	.01	.19
Side-striped jackal	.02						.00	.00	.00
Aardwolf	.00							.00	.00
Ratel	.00								.00
Bat-eared fox	.19								

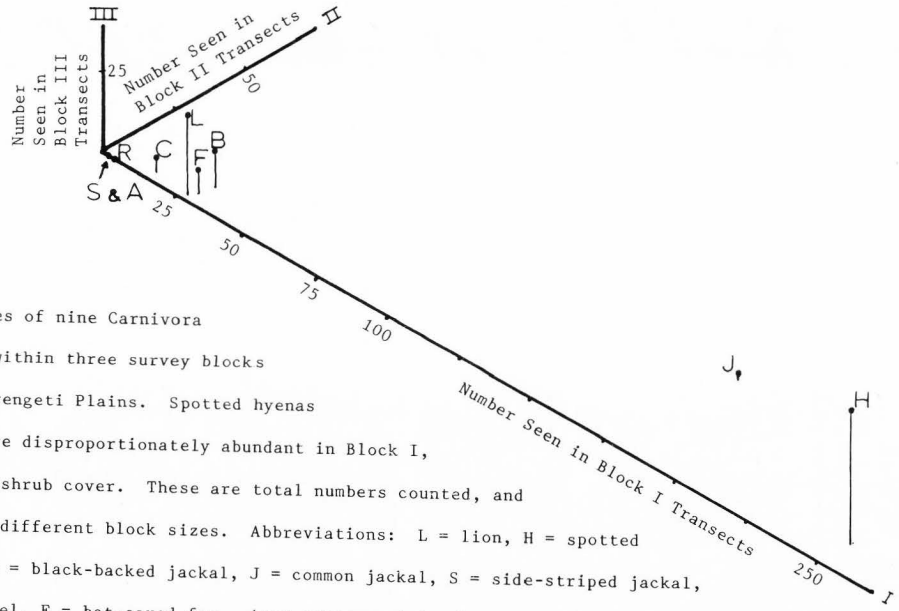


Figure 4.3 Abundances of nine Carnivora in survey transects within three survey blocks year-round on the Serengeti Plains. Spotted hyenas and common jackals are disproportionately abundant in Block I, the area of greatest shrub cover. These are total numbers counted, and are not adjusted for different block sizes. Abbreviations: L = lion, H = spotted hyena, C = cheetah, B = black-backed jackal, J = common jackal, S = side-striped jackal, A = aardwolf, R = ratel, F = bat-eared fox. Axes correspond to the survey blocks shown in Figure 5.1. The blocks are described in Section 4.2. Data are from Appendix E.

jackal) are compared along one niche axis representing food types. The data are the frequencies with which each prey species or food type was caught, scavenged, or foraged. The most consistent, large data set available for interspecific comparisons is that of Appendix F, although it permits comparisons of only five of the seven species. Comparison of all seven ungulate-eating Carnivora is achieved by combining Appendices F, J, K, and L, although some consistency is lost in doing so. The total of 64 different resource states, where each resource state is a prey species, contains 4,171 observations of food types that were recorded as captured, scavenged, or foraged. These data and their published sources are listed in the Appendices. Commonly killed prey sometimes were not recorded, because observers considered the event unnoteworthy, e.g. lion kills of wildebeest and zebra (Kruuk and Turner 1967:7-8). Also, small prey tend to be under-reported because of the speed with which they are eaten. Some possible duplication of reported observations among authors may pose another problem.

Through cluster analysis (Fig. 4.4), comparison of the seven Carnivora showed that cheetahs and black-backed jackals are most similar in the prey species they ate. The leopard is the next most-similar carnivore. The resemblance matrix and cophenetic correlation coefficient are in Table I.2 (Appendix I).

Non-circular niche metrics (Table 4.2) show that lions have the most generalized diet, i.e. they eat the greatest variety of species, as measured by the largest niche breadth. Black-backed jackals and common jackals have the most-similar diets with regard to prey species and food types eaten, as measured by the largest niche overlap. Lions and spotted hyenas show the next greatest similarity in prey species

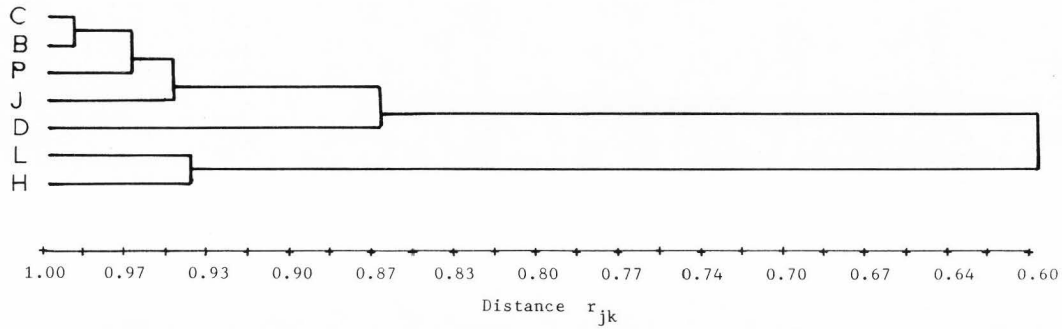


Figure 4.4 Dendrogram of seven Carnivora, showing similarity in year-round use of 64 food types. Abbreviations: L = lion, H = spotted hyena, C = cheetah, P = leopard, D = African wild dog, B = black-backed jackal, J = common jackal. Data are from Appendices F, J, K, and L.

Table 4.2 Niche breadths and niche overlaps year-round among all seven ungulate-eating Carnivora. Calculated from prey species and other food types eaten. Abbreviations: H = spotted hyena, C = cheetah, P = leopard, D = African wild dog, B = black-backed jackal, J = common jackal.

Carnivora Species	Niche Breadths	Pairwise Niche Overlaps					
		H	C	P	D	B	J
Lion	.51	.98	.72	.78	.95	.82	.81
Spotted hyena	.39		.63	.71	.91	.76	.75
Cheetah	.21			.97	.84	.96	.94
Leopard	.33				.91	.96	.96
African wild dog	.42					.92	.91
Black-backed jackal	.35						.99
Common jackal	.39						

eaten.

Graphical comparison (Fig. 4.5) shows that lions and spotted hyenas feed mainly on wildebeest and zebras, whereas the other five predators feed mostly on Thomson's gazelles. African wild dogs, however, are somewhat intermediate. The differences in frequency of occurrence of six prey types utilized by lion, spotted hyena, cheetah, leopard, African wild dog, black-backed jackal, and common jackal are statistically significant (X^2=1,474.41, df = 30, $p < 0.001$, two-tailed).

4.4 Five Largest Carnivora

This analysis of interspecific one-dimensional niches includes only the data in Appendix F, because they are more comparable. The five Carnivora considered are: lion, spotted hyena, cheetah, leopard, and African wild dog. This axis comprises 47 resource states, each state being a prey or food type that was recorded captured, scavenged, or foraged. The total number of observations is 3,922, which is 94% of the data used in Section 4.3.

Through cluster analysis (Fig. 4.6), comparison of the five largest Carnivora shows that leopard and cheetah are most similar in the prey species they eat. The resemblance matrix and cophenetic correlation are in Table I.3 (Appendix I).

Non-circular niche metrics (Table 4.3) show that lions have the most generalized diet, as measured by the largest niche breadth. Lion and spotted hyena, as well as cheetah and leopard, are the species dyads that have the most-similar diet, as measured by the largest niche overlap.

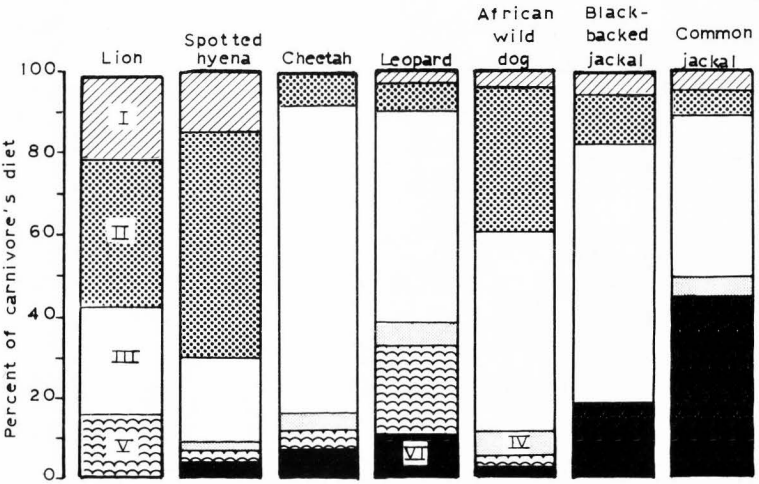


Figure 4.5 Percent frequencies year-round in which seven Carnivora utilized six prey types. Prey items comprising more than zero but less than 2% of a carnivore's diet are omitted, therefore each bar may not represent 100%. Abbreviations: I = zebra, II = wildebeest, III = Thomson's gazelle, IV = Grant's gazelle, V = all other ungulates, VI = all non-ungulates. Data are from Appendices F, J, K, and L.

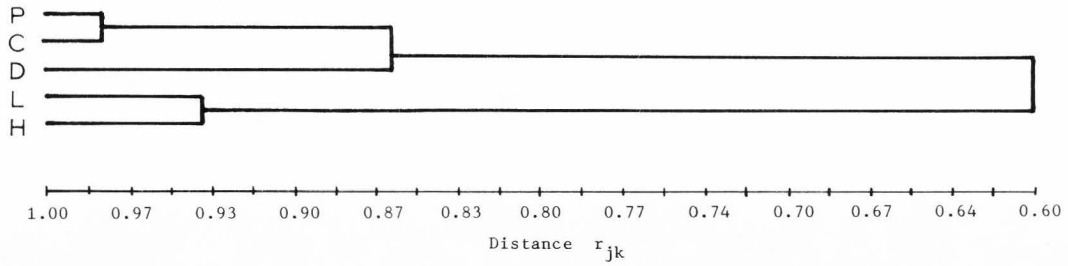


Figure 4.6 Dendrogram of five Carnivora, showing similarity in year-round use of 47 food types. Abbreviations: L = lion, H = spotted hyena, C = cheetah, P = leopard, D = African wild dog. Data are from Appendix F.

Table 4.3 Niche breadths and niche overlaps year-round among the five largest Carnivora. Calculated from prey species and other food types eaten.

Carnivora Species	Niche Breadths	Pairwise Niche Overlaps			
		H	C	P	D
Lion	.61	.98	.73	.78	.95
Spotted hyena	.44		.63	.71	.90
Cheetah	.24			.98	.85
Leopard	.39				.91
African wild dog	.50				

Graphical comparisons of the frequencies by which the five carnivores utilize the prey types are nearly identical to those in Figure 4.5, so the graph is not shown. The differences in frequency of occurrence of the same six prey categories used in Section 4.3 by lion, spotted hyena, cheetah, leopard, and African wild dog are statistically significant (X^2= 1,154.90, df = 20, $p < 0.001$, two-tailed).

Comparison of the prey species captured or scavenged (Table 4.4) shows that cheetahs and African wild dogs specialize on fewer prey species. Lion, spotted hyena, and leopard each fed on 24 prey species, although some of the prey species differed, while only 16 prey species were recorded for cheetah and 17 for wild dog. When adjusted for the number of observations, leopard is by far the most generalized as measured by the number of prey species selected.

4.5 Lion, Spotted Hyena, Cheetah, and African Wild Dog

Four Carnivora--lion, spotted hyena, cheetah, and African wild dog--are compared along 11 niche axes. The data are from all sightings of these carnivores during 1,003 hare censuses carried out between 12 July 1977 and 6 February 1978. The Carnivora were recorded regardless of whether they were within or outside the census transects. No leopard was sighted during any of these censuses. Jackals, although numerous, were not recorded, nor were other Carnivora. A new census transect was begun every time one variable changed on any of the 11 resource axes. Further details of the hare censuses were described by G.W. Frame and F.H. Wagner (1981).

The 11 axes and number of resource states recorded for each Carnivora sighting are the following: 10 resource states for time of

Table 4.4 Percent occurrence of prey species captured or scavenged most often year-round by the five species of large Carnivora, including a generalist index.

Prey Species[2]	Percent Occurrence[1]				
	Lion	Spotted Hyena	Cheetah	Leopard	African Wild dog
Thomson's gazelle	26	20	75	54	49
Wildebeest	36	58	8	7	35
Zebra	21	15	1	3	4
Grant's gazelle	1	2	4	6	6
African buffalo	6	-	-	-	-
Topi	3	-	-	2	-
Hares	-	-	6	-	-
Bohor reedbuck	-	-	1	11	-
Warthog	2	-	-	-	1
Impala	-	-	2	4	-
Kongoni	-	-	1	-	-
Eland	1	-	-	-	-
Giraffe	1	-	-	-	-
European stork	-	-	-	3	-
Baboon	-	-	-	2	-
Total percent	97	95	98	92	95
Sample size	1,399	811	495	219	998
Number of species	24	24	16	24	17
Generalist index[3]	1.7	3.0	3.2	11.0	1.7

1 Percent occurrence is shown only if the prey species constituted 1.0 percent or more of the sample for that species of Carnivora.

2 Prey species are listed in order of decreasing importance as measured by the frequency with which they were observed being eaten by all five Carnivora species combined.

3 The "generalist index" is calculated as follows: (Number of prey species in the sample) ÷ (Sample size ÷ 100) = Number of prey species recorded per 100 observations.

day, 8 for habitat, 3 for weather, 2 for moonlight, 3 for condition of the grass, 3 for availability of water, 3 each for availability of Thomson's gazelles and wildebeest, and 2 each for the presence of hares, ostriches, and warthogs. Data for the entire seven-month period are given by season in Appendix M, but are combined in the present analysis to represent year-round use. No observation was recorded for any of the four species in one of the time-of-day categories, so that category was deleted from the analysis. Using the marginal totals of the data, this leaves 40 resource states, containing 5,333 observations on 11 axes. All 11 axes are used, because I believe they are useful indices of prey distribution and availability, both of which influence the Carnivora.

The analysis is repeated on a reduced data set to address the issue of whether or not the inclusion of data from questionable categories substantially changes the results. The four axes omitted are the condition of the grass, and the occurrence of hares, ostriches, and warthogs. The reduced data set comprises 31 resource states, containing 3,237 observations on seven axes.

The comparison through cluster analysis (Fig. 4.7) shows that lions and spotted hyenas are most similar in their distribution on the Serengeti Plains when measured by the 11 environmental variables. This analysis uses the marginal totals only (cf. Section 3.2.b). The resemblance matrix and cophenetic correlation are in Table I.4 (Appendix I).

Niche metrics of the full data set show that spotted hyenas are the generalists, as indicated by their largest niche breadth (Table 4.5). Lions and cheetahs are most similar in their occurrence, as measured by

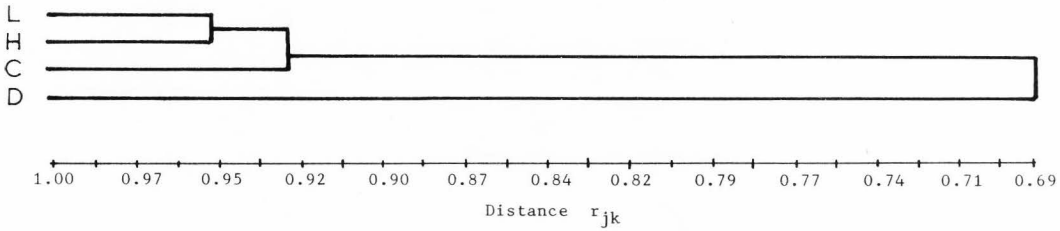


Figure 4.7 Dendrogram of lion, spotted hyena, cheetah, and African wild dog, showing similarity in year-round occurrence in 40 resource states on 11 niche axes. Computed from marginal totals. Abbreviations: L = lion, H = spotted hyena, C = cheetah, D = African wild dog. Data are from Appendix M.

Table 4.5 Niche-breadth relationships year-round among lion, spotted hyena, cheetah, and African wild dog, calculated by three methods. Species are listed in order of decreasing non-circular niche breadth. The three methods of calculation are used on the combined seasonal data in Appendix M; the mathematical results are in Table N.1 of Appendix N. Abbreviations: L = lion, H = spotted hyena, C = cheetah, D = African wild dog.

Relative Niche Breadth	Full Data Set: Axes I to XI			Reduced Data Set: Axes I to IV and VI to VIII		
	Product Method	Summation Method	Projection Method	Product Method	Summation Method	Projection Method
Widest breadth	H	H	H	H	H	H
	L	L	C	C	L	C
	C	C	L	L	C	L
Narrowest breadth		D	D		D	D
Zero breadth	D			D		

the largest niche overlap (Table 4.6). Niche metrics of the reduced data set give the same results (Tables 4.5 and 4.6). The mathematical results are in Appendix N.

Comparisons are made of the 5 out of 11 niche axes where statistically significant differences exist in the occurrence of lions, spotted hyenas, and cheetahs among the resource states. On all 11 axes the African wild dogs are omitted because of inadequate sample sizes for meeting the test criteria of minimum expected cell frequencies. Lions and spotted hyenas appear to be similar in being active at night and in staying closer to migratory prey, whereas spotted hyenas and cheetahs seem similar in their use of cover. The results for each axis are the following:

Axis I comprises the time of day that carnivores were sighted. The differences in frequency of occurrence of the three times of day when lions, spotted hyenas, and cheetahs were sighted are statistically significant ($X^2 = 13.77$, df = 4, $p < 0.01$, two-tailed). The percent frequencies with which these three carnivores were seen during the three times of day are:

Lions 46% dawn to 0900 hr, 48% 0901 hr to sunset, and 6% dusk to 0300 hr;

Spotted hyenas 57% dawn to 0900 hr, 33% 0901 hr to sunset, and 10% dusk to 0300 hr;

Cheetahs 58% dawn to 0900 hr, and 42% 0901 hr to sunset.

Axis II comprises the cover quality of the habitat where carnivores were sighted. The three habitat types are: no cover (short grasses with herbs mainly of Solanum sp. or Hypoestes sp.), moderate cover (medium grasses, or short grasses with shrubs of Indigofera basiflora

Table 4.6 Niche overlap relationships year-round among lion, spotted hyena, cheetah, and African wild dog, calculated by three methods. Species pairs are listed in order of decreasing non-circular niche overlap. The three methods of calculation are used on the combined seasonal data in Appendix M; the mathematical results are in Table N.2 of Appendix N. Abbreviations: L = lion, H = spotted hyena, C = cheetah, D = African wild dog.

Relative Niche Overlap	Full Data Set: Axes I to XI			Reduced Data Set: Axes I to IV and VI to VIII		
	Product Method	Summation Method	Projection Method	Product Method	Summation Method	Projection Method
Greatest overlap		LC	LC		LC	LC
		LH	HC		LH	HC
		HC	LH		HC	LH
		CD	HD		CD	HD
		LD	LD		LD	LD
Least overlap		HD	CD		HD	CD
Zero overlap	LH			LH		
	LC			LC		
	LD			LD		
	HC			HC		
	HD			HD		
	CD			CD		

or Justicia elliotii), and dense cover (woodlands, riverine forests, and thickets on kopjes). The differences in frequency of occurrence of three densities of vegetative cover where the three Carnivora were sighted are statistically significant ($X^2 = 21.18$, df = 4, $p < 0.001$, two-tailed). The percent frequencies with which these three carnivores were seen among the three cover types are:

Lions 7% no cover, 31% moderate cover, and 62% dense cover;

Spotted hyenas 12% no cover, 53% moderate cover, and 35% dense cover;

Cheetahs 8% no cover, 52% moderate cover, and 40% dense cover.

Axes III and IV comprise the weather and the occurrence of moonlight at the time the carnivores were sighted. The test criterion of minimum expected cell frequencies was not met on either axis.

Axis V comprises the greenness of the grassland. The three grassland condition categories (desiccated, slightly green, and green) serve as indicators of prey availability, because many large grazers move in response to the condition of the grasses and forbs. The differences in frequency of occurrence of the three greenness categories where lions, spotted hyenas, and cheetahs were sighted are statistically significant ($X^2 = 28.7$, df = 4, $p < 0.001$, two-tailed). The percent frequencies with which these three carnivores were seen among the three greenness categories are:

Lions 13% desiccation, 35% slightly green, and 52% green;

Spotted hyenas 5% desiccation, 33% slightly green, and 62% green;

Cheetahs 23% desiccation, 32% slightly green, and 45% green.

Axis VI comprises the presence or absence of water within 3 km of

where the carnivore was sighted. The differences in frequency of occurrence of the two water categories where lions, spotted hyenas, and cheetahs were sighted are statistically significant ($X^2 = 11.64$, df = 2, $p < 0.01$, two-tailed). The percent frequencies with which these three carnivores were seen between the two water-availability categories are:

Lions 26% no water and 74% water present;

Spotted hyenas 33% no water and 67% water present;

Cheetahs 52% no water and 48% water present.

Axis VII comprises the availability of Thomson's gazelles. The differences in frequency of occurrence of the three densities of Thomson's gazelles where lions, spotted hyenas, and cheetahs were sighted are statistically significant ($X^2 = 15.44$, df = 4, $p < 0.01$, two-tailed). The percent frequencies with which these three carnivores were seen among the three gazelle-availability categories are:

Lions 18% no gazelles, 49% few, and 33% many;

Spotted hyenas 14% no gazelles, 47% few, and 39% many;

Cheetahs 30% no gazelles, 50% few, and 20% many.

Test results for Axes VIII through XI show no statistically significant differences at $p = 0.01$ (the acceptable p-level stated in Section 3.2.d). The axes are the frequency of sightings of lions, spotted hyenas, and cheetahs among three densities of wildebeest ($X^2 = 11.38$, df = 4, $p < 0.05$, two-tailed), and the presence or absence of hares ($X^2 = 2.78$, df = 2, $p < 0.30$, two-tailed), ostriches ($X^2 = 0.72$, df = 2, $p < 0.70$, two-tailed), and warthogs ($X^2 = 2.86$, df = 2, $p < 0.30$, two-tailed).

The relative frequencies by which these Carnivora captured and scavenged food are shown in Table 4.7. The percentages are calculated

from the following sources: Lions (Schaller 1972:213 and his Table 39), spotted hyenas (Kruuk 1972a: his Table 26), cheetahs and African wild dogs (Appendix O). Spotted hyenas and lions appear to be important scavengers.

Table 4.7 Percent occurrence of obtaining food year-round by capturing and by scavenging among lion, spotted hyena, cheetah, and African wild dog.

Food Sources	Percent Occurrence			
	Lion	Spotted Hyena	Cheetah	African Wild Dog
Captured	75	61	98	90
Scavenged	16	20	1	6
Uncertain	9	19	1	4

4.6 Lion, Cheetah, and African Wild Dog

Lions, cheetahs, and African wild dogs are compared by the resource states they occupied on five axes while hunting and eating. The axes are time of day, time of night, vegetative cover type, prey species, and scavenging. Data for all three species are from Schaller (1972) and additional data for cheetahs (G.W. Frame and L.H. Frame, in prep.) and African wild dogs (L.H. and G.W. Frame, unpubl. data) are from Appendix Q. They are listed in Appendix H in their combined form for

this analysis. The 34 resource states on five axes include 5,596 observations.

Circular niche metrics show that lions are the relative generalists in their hunting behavior and ecology, as indicated by the widest niche breadth (Table 4.8). That is, lions take a wide variety of foods in many different times and habitats. By these same measures of hunting behavior and ecology, cheetahs and African wild dogs are more similar to each other than they are to lions, as indicated from the greatest niche overlap (Table 4.9). The mathematical results are in Appendix P.

Table 4.8 Niche-breadth relationships year-round among lion, cheetah, and African wild dog, calculated by three methods. Species are listed in order of decreasing circular niche breadth. The three methods of calculation are used on the data in Appendix H; the mathematical results are in Table P.1 of Appendix P. Abbreviations: L = lion, H = spotted hyena, C = cheetah, D = African wild dog.

Relative Niche Breadth	Product Method	Summation Method	Projection Method
Widest breadth	L	L	C
	D	C	L
Narrowest breadth	C	D	D

Table 4.9 Niche-overlap relationships year-round among lion, cheetah, and African wild dog, calculated by three methods. Species pairs are listed in order of decreasing circular niche overlap. The three methods of calculation are used on the data in Appendix H; the mathematical results are in Table P.2 of Appendix P. Abbreviations: L = lion, H = spotted hyena, C = cheetah, D = African wild dog.

Relative Niche Overlap	Product Method	Summation Method	Projection Method
Greatest overlap	CD	CD	CD
	LC	LC	LD
Least overlap	LD	LD	LC

Comparisons are made of the 4 out of 5 niche axes where statistically significant differences exist. Cheetahs and African wild dogs appear more similar to each other than they are to lions, by hunting later in the daytime, by hunting in open vegetative cover, by rarely hunting zebras, and by seldom scavenging. The results for each axis are:

Axis I comprises the daytime hours when carnivores were recorded hunting or eating (Fig. 4.8). The differences in frequency of occurrence of the four times of day when lions, cheetahs, and African wild dogs were recorded hunting or eating are statistically significant ($\chi^2 = 147.51$, df = 6, $p < 0.001$, two-tailed).

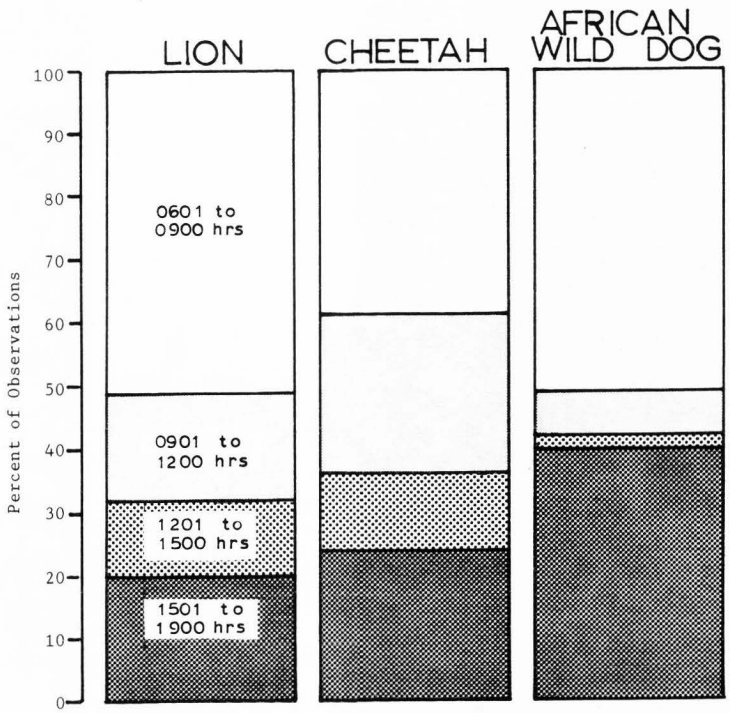


Figure 4.8 Percent frequencies year-round in which lion, cheetah, and African wild dog hunted or ate in four daytime periods. Data are from Appendix H.

Axis II comprises the nighttime hours when carnivores were recorded hunting or eating. The test criteria of minimum expected cell frequencies is not met. Thus, it can not be shown that there is any non-random separation of carnivore species along the nighttime hunting-eating axis.

Axis III comprises the physiognomic vegetation types among which carnivores were recorded hunting or eating (Fig. 4.9). The five vegetative cover categories are: no cover (short grasses, sometimes with herbs of Hypoestes or Solanum), slight cover (mosaic of short and medium grasses), moderate cover (medium grasses or any grasses with shrubs of Indigofera or Justicia), dense cover (bushes or thickets on kopjes), and tall cover (woodlands or riverine forests). The differences in frequency of occurrence of the five vegetation types where lions, cheetahs, and African wild dogs were recorded hunting or eating are statistically significant ($X^2 = 539.17$, $df = 8$, $p < 0.001$, two-tailed).

Axis IV comprises the major migratory prey species that carnivores were recorded hunting or eating. The differences in frequency of occurrence by which the three prey species were hunted or eaten by lions, cheetahs, and African wild dogs are statistically significant ($X^2 = 135.75$, $df = 4$, $p < 0.001$, two-tailed). The percentage frequencies in which the three carnivores were recorded hunting or eating the three prey species are:

Lions 20% zebras, 26% wildebeest, and 54% Thomson's gazelles;

Cheetahs 3% zebras, 18% wildebeest, and 79% Thomson's gazelles;

Wild dogs < 1% zebras, 42% wildebeest, and 58% Thomson's gazelles.

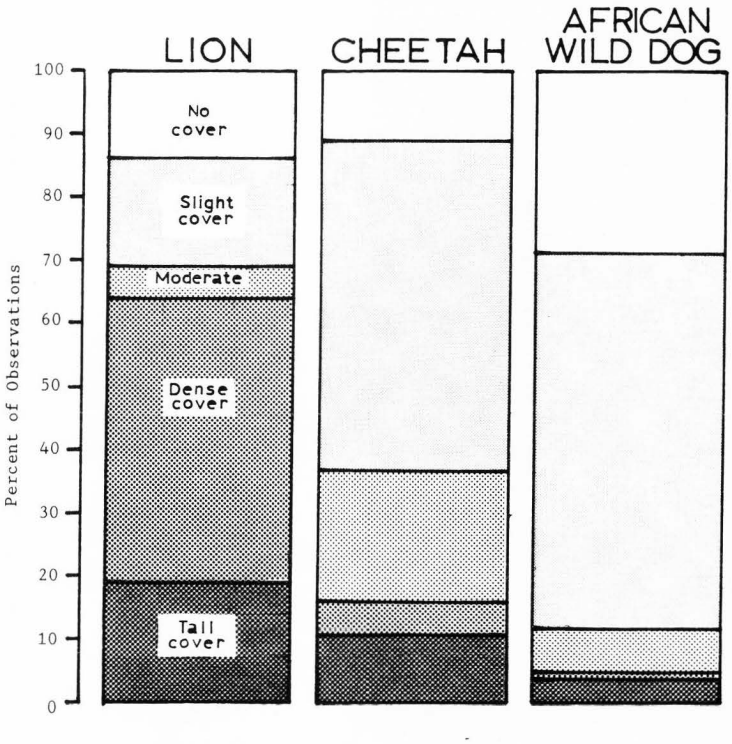


Figure 4.9 Percent frequencies year-round in which lion, cheetah, and African wild dog hunted or ate in five vegetative cover types. Data are from Appendix H.

Axis V comprises the methods of obtaining food, i.e. capturing versus scavenging prey, that carnivores were recorded hunting or eating. The differences in frequency of occurrence of capturing prey and scavenging prey by lions, cheetahs, and African wild dogs are statistically significant ($X^2 = 70.55$, df = 2, $p < 0.001$, two-tailed). Lions scavenged 18% of their meals, African wild dogs 6%, and cheetahs < 1%.

4.7 Cheetah and African Wild Dog

Cheetahs and African wild dogs are compared by 78 resource states on nine niche axes during their hunts (Appendix Q). The total number of observations is 6,251. Data were recorded during 495 successful and unsuccessful hunts by cheetahs (G.W. Frame and L.H. Frame, in prep.) and 512 successful hunts by African wild dogs (L.H. and G.W. Frame, unpubl. data). Scavenging is included for both species. Unsuccessful hunts by African wild dogs are not included, because they tend to hunt in an activity period containing a series of unsuccessful hunts terminating in a successful one, whereas cheetahs often undergo only one hunt (successful or unsuccessful) at a time followed by a rest or waiting period.

Circular niche metrics show that African wild dogs are less specialized in hunting than cheetahs are, as indicated by the wider niche breadth. But there are many similarities, as indicated by the large niche overlap. The summation method gives niche breadths of 0.65 for cheetah and 0.74 for African wild dogs, with an overlap of 0.79. Mathematical results for each axis, calculated in three ways, are in Appendix R.

Comparisons are made of the nine axes where statistically significant differences exist. Cheetahs and African wild dogs appear similar, because half their diets consist of Thomson's gazelles. There are, however, important behavioral differences which tend to separate their hunting in time and place. The results for each axis are:

Axis I Comprises the physiognomic vegetation type in which hunting was observed. The five vegetative cover categories are: no cover (short grasses sometimes with herbs of Hypoestes or Solanum), slight cover (mosaic of short and medium grasses), moderate cover (medium grasses or any grasses with shrubs of Indigofera or Justicia), dense cover (bushlands or thickets on kopjes), and tall cover (woodlands or riverine forests). The differences in frequency of occurrence of five vegetation types where cheetahs and African wild dogs hunted are statistically significant ($X^2 = 97.00$, df = 4, $p < 0.001$, two-tailed). The percent frequencies in which cheetahs and African wild dogs were recorded hunting in the five vegetation types are:

Cheetahs 11% no cover, 52% slight cover, 20% moderate cover, 6% dense cover, and 11% tall cover;

African wild dogs 29% no cover, 59% slight cover, 7% moderate cover, 1% dense cover, and 4% tall cover.

Axis II comprises the hour of the day or night in which each hunt was observed, or, in the case of longer hunts, the hour in which the most active part of the hunt occurred. The differences in frequency of occurrence of the five times of day when cheetahs and wild dogs hunted are statistically significant ($X^2 = 116.46$, df = 4, $p < 0.001$, two-tailed). The precent frequencies with which these two carnivores were seen hunting during five diel time periods are:

Cheetahs 37% 0601-0900 hr, 26% 0901-1200 hr, 16% 1201-1600 hr, 20% 1601-1900 hr, and 1% 1901-0600 hr;

African wild dogs 43% 0601-0900 hr, 8% 0901-1200 hr, 4% 1201-1600 hr, 35% 1601-1900 hr, and 10% 1901-0600 hr.

Axis III comprises the abundance of prey where the hunting was observed. The differences in frequency of occurrence of the four prey densities during hunts by cheetahs and African wild dogs are statistically significant ($X^2 = 131.72$, df = 3, $p < 0.001$, two-tailed). The percent frequencies with which these two carnivores were seen hunting in the four abundances of prey are:

Cheetahs 19% none or few prey, 50% moderate prey, 22% abundant prey, and 9% migrations;

African wild dogs 6% none or few, 22% moderate, 42% abundant, and 30% migrations.

Axis IV comprises the weather at the time hunting was observed. The two weather categories are no rain (sunny or clear or cloudy) and rain. The differences in frequency of occurrence of the two weather types when cheetahs and African wild dogs hunted are statistically significant ($X^2 = 14.90$, df = 1, $p < 0.001$, two-tailed). Nearly 10% of the African wild dog hunts and 2% of the cheetah hunts were in wet weather.

Axis V comprises the prey group sizes that were hunted. The differences in frequency of occurrence of the seven prey group-sizes that cheetahs and African wild dogs hunted are statistically significant ($X^2 = 80.24$, df = 6, $p < 0.001$, two-tailed). The percent frequencies with which cheetahs and wild dogs were seen hunting each prey group size are:

Cheetahs 40% lone prey, 11% two prey animals, 10% 3-5 prey, 9% 6-10 prey, 7% 11-20 prey, 19% 21-100 prey, and 4% 101 or more prey;

African wild dogs 32%, lone prey, 4% two, 5% 3-5, 4% 6-10, 5% 11-20, 20% 21-100, and 30% 101 or more.

Axis VI comprises the use of stalking versus no stalking during hunting. The differences in frequency of occurrence of stalking or not during hunts by cheetahs and African wild dogs are statistically significant ($X^2 = 96.92$, df = 1, $p < 0.001$, two-tailed). Cheetahs stalked during 77% of their hunts and African wild dogs stalked during 35%.

Axis VII comprises the distances that prey were chased during hunts. The differences in frequency of occurrence of the six chase lengths during hunts by cheetahs and African wild dogs are statistically significant ($X^2 = 135.00$, df = 5, $p < 0.001$, two-tailed). The percent frequencies with which cheetahs and African wild dogs were seen chasing their prey in the six distance categories are:

Cheetahs 10% 0-10 m, 45% 11-100 m, 37% 101-300 m, 4% 301-500 m, 3% 501-1,000 m, and 0% > 1,000 m;

African wild dogs 11% 0-10 m, 9% 11-100 m, 14% 101-300 m, 11% 301-500 m, 21% 501-1,000 m, and 34% > 1,000 m.

Axis VIII comprises the use of prey catching and scavenging as methods of obtaining food. The differences in frequency of occurrence of prey catching versus scavenging during food-getting by cheetahs and African wild dogs are statistically significant ($X^2 = 11.20$, df = 1, $p < 0.001$, two-tailed). Cheetahs scavenged about 1% of their meals and African wild dogs 6%.

Axis IX comprises the prey species that were hunted or eaten. The differences in frequency of occurrence of the seven prey species or types that were hunted by cheetahs and African wild dogs are statistically significant ($X^2 = 137.23$, df = 6, $p < 0.001$, two-tailed). The percent frequencies with which cheetahs and African wild dogs were seen hunting or eating these prey are:

Cheetahs 4% zebra, 10% wildebeest, 9% Grant's gazelle, 59% Thomson's gazelle, 6% hare, 8% other ungulates, and 4% other types of food;

African wild dogs < 1% zebra, 37% wildebeest, 6% Grant's gazelle, 51% Thomson's gazelle, < 1% hare, 2% other ungulates, and 3% other types of food.

4.8 Black-backed Jackal and Common Jackal

Black-backed jackals were compared with common jackals using the data in Lamprecht (1978a: his Table 2). The following seven food categories, or resource states, were used: big game, small game, small mammals, birds, total arthropods, total vegetable matter, and trash. The number of times that a fecal sample contained identifiable remains corresponding to each of these categories was calculated from the sample size and percent frequency data in Lamprecht's table. These count data are presented by season in Appendix S.

Circular niche metrics suggest that black-backed jackals are slightly more generalized in their food habits than are the common jackals, as indicated by their slightly wider niche breadth, but the difference is so slight that there might be no real difference. However, these two jackals have highly similar food habits, as

indicated by the very large niche overlap. The niche breadth is 0.87 for black-backed jackals and 0.85 for common jackals, with an overlap of 0.91.

Visual assessment of the food axis suggests that black-backed jackals tend to eat bigger foods than do the common jackals. The differences in frequency of occurrence of four food types in the diets of the two jackal species year-round are statistically significant ($X^2 = 22.06$, $df = 3$, $p < 0.001$, two-tailed). The percent frequencies with which the fecal samples of the two jackals contained items in the four combined food categories are:

Black-backed jackals 36%, ungulates, 8% small mammals and birds, 16% arthropods, and 40% plants and trash;

Common jackals 19% ungulates, 11% small mammals and birds, 45% arthropods, and 25% plants and trash.

4.9 Discussion

The results of the present chapter provide a picture of which Carnivora species are most specialized, and which species are most similar, in their use of the measured resources. Measurements were taken throughout the entire year, and most are from the entire ecosystem. Exploitation competition is most likely to occur when a high degree of similarity exists and resources are limited.

The following paragraphs discuss the Carnivora one at a time:

Lions are the most generalized feeders among the ungulate-eaters, with regard to prey species hunted and food types foraged year-round throughout the Serengeti ecosystem (Tables 4.2 and 4.3). When compared by distribution among habitat types and prey availability, lions are

very similar to spotted hyenas and cheetahs, but quite different from African wild dogs (Fig. 4.7). Measured by prey species hunted, the lion and spotted hyena are most similar to each other and far removed from the other ungulate-eaters (Figs. 4.4 and 4.6). Among four large Carnivora, lions and cheetahs show the most similar distribution among habitat types and prey occurrences (Table 4.6). The greatest similarity in kinds of prey species or food types caught, scavenged, or foraged by five Carnivora is tied between the dyad of lion and spotted hyena and the dyad of cheetah and leopard (Table 4.3).

Spotted hyenas show the most ubiquitous distribution with regard to habitat types and prey availability year-round throughout the ecosystem (Tables 4.1 and 4.5). Among the seven ungulate-eaters, spotted hyenas are most similar to black-backed jackals (Fig. 4.2) and to common jackals (Table 4.1) in their distribution on the Serengeti Plains. Spotted hyenas are the most abundant of the nine large and medium-sized Carnivora sighted during the transect surveys in habitats ranging from woodland to short grass plains (Fig. 4.3). The niche analyses from this chapter show great similarities in resource use among the same species dyads, which are suggestive of actual or potential competition.

Cheetahs are more similar to African wild dogs than they are to lions, when compared in time, habitat, prey species hunted, and scavenging behavior year-round throughout the ecosystem (Section 4.6). Cheetahs are most specialized in catching their own food, as opposed to scavenging, compared to lions, spotted hyenas, and African wild dogs (Table 4.7).

Leopards were consistently absent from surveys on the distribution of ungulate-eaters year-round in the Serengeti Plains portion of the

ecosystem (Appendices E and M). This might be due in part to their relatively low abundance (Table 2.1). More importantly, however, it appears to be a result of the leopard's nocturnal activity and preference for dense woodlands and riverine vegetation. When compared to the other ungulate-eaters according to prey species hunted, leopards are most similar to cheetahs and black-backed jackals (Figs. 4.4 and 4.6). Based only on prey species eaten, leopards appear to be most similar to cheetahs (Fig. 4.5). In terms of the kinds of prey species or food types caught, scavenged, or foraged by five Carnivora (lion, spotted hyena, cheetah, leopard, African wild dog), leopards are most similar to cheetahs (Fig. 4.5). In terms of the kinds of prey species or food types caught, scavenged, or foraged by five Carnivora (lion, spotted hyena, cheetah, leopard, African wild dog), leopards are most similar to cheetahs (Table 4.3). As measured by the generalist index among the five largest Carnivora (Table 4.4), leopards are by far the most generalized in their selection of prey species.

African wild dogs are the generalist species year-round, throughout the ecosystem, when compared only with cheetahs and lions for habitat use, time of hunting, prey species hunted, and scavenging behavior (Sections 4.6 and 4.7). In other comparisons of prey species eaten, the African wild dogs are second only to lions as generalists (Tables 4.2 and 4.3).

The black-backed jackals and common jackals are second only to spotted hyenas in their ubiquitous occurrence among major vegetation types year-round, throughout the Serengeti Plains portion of the ecosystem (Table 4.1). These two jackals show the most similarity among seven Carnivora in prey species or types caught, scavenged, or

foraged (Fig. 4.4 and Table 4.2).

Elsewhere, there is little information available pertaining to the measurements of niche breadths and overlaps of African carnivores. However, a study in the Mkomazi Game Reserve, Tanzania, found that, among the several carnivores that were considered, lions had the largest niche breadth with regard to habitat and season (Harris 1972). In the Tarangire National Park, Tanzania, cheetahs and African wild dogs were shown to be similar in their use of grassland and open woodland, while leopards were more specific to open woodland and dense woodland, and lions were intermediate (Lamprey 1963). The results are similar, in general, to the findings in the Serengeti.

This chapter provides generalized descriptions of year-round ecological relationships among the ungulate-eating Carnivora in the Serengeti ecosystem. These niche relationships must always be viewed in the context of the particular resources or behaviors that are measured. The niche descriptions and their usefulness are discussed further in Chapter Fourteen.

CHAPTER V

INTERSPECIFIC YEAR-ROUND NICHES OF VULTURES

5.1 Similarity Suggests Competition

My working hypothesis is that the pairs of vulture species most similar in their use of the ungulate food resource are most likely to compete at least occasionally. This chapter, therefore, identifies which species of vulture are most similar in their use of the resources.

Competition among vultures in the Serengeti ecosystem has been investigated several times (Petrides 1959; Kruuk 1967; Houston 1975a, 1980). Cody (1974:204-206) used Kruuk's (1967) vulture data to show that interspecific dominance affects access to food. Because 10 to 80 or more vultures of the six species feed together on discrete food items in the Serengeti, they appear to be competing.

5.2 Six Vultures

I first describe vulture niches by using the data recorded for scavengers on cheetah-killed prey. Of the 495 recorded cheetah hunts, 219 resulted in capture, kill, or eating. Notes of avian scavengers were recorded on 57% of these successful hunts, with vultures absent on 39 occasions and present on 86. The niche data of 22 resource states on six axes are listed in the first half of Appendix T.

I did a second description by combining these observations with data from other sources. The additional data provide a more complete

picture of vulture behavior and ecology, but the disadvantage is a lack of consistency in when and how the data from the several different sources were collected. The original six axes of data from vultures scavenging on cheetah-killed prey are used again, but four axes are added. The first added axis, comprising five resource states representing the carcass part that each species of vulture scavenged, has the number of observations in each category calculated as closely as possible from the graphs in Kruuk (1967: his Fig. 2). The second added axis comprises four resource states, representing the sequence of arrival at the carcass (data from Kruuk 1967: his Fig. 3). The third added axis comprises four resource states representing the occurrence of two species together (data from Houston 1980: his Table 3). And the fourth added axis comprises five resource states representing the size of the carcass on which the vultures fed (data from Houston 1980: his Table 4). Thus a total of 40 resource states on 10 axes (all of Appendix T) are used in this second analysis. The total number of observations is 4,062.

Comparison of six vultures on all ten niche axes shows, through cluster analysis (Fig. 5.1), that the Rüppell's vulture and lappet-faced vulture are most similar in their feeding behavior and ecology. This analysis is done on the marginal totals only (cf. Section 3.2.b). The resemblance matrix and cophenetic correlation coefficient are in Table I.5 (Appendix I).

Non-circular niche metrics are computed in three ways for additional comparison, but the results of the summation method (cf. Section 3.2.c) are accepted as giving the best estimate. The first analysis (that of scavenging only from cheetah-killed prey) shows that

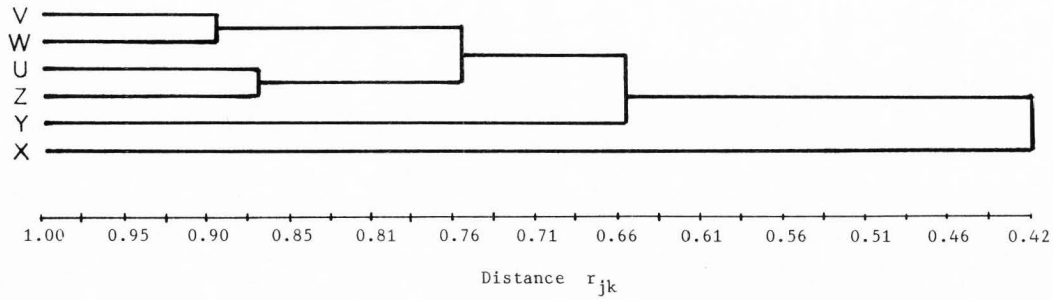


Figure 5.1 Dendrogram of six species of vulture, showing similarity in year-round feeding behavior and ecology at carcasses. Measurements are of 40 resource states on 10 niche axes. Computed from marginal totals. Abbreviations: U = African white-backed, V = Rüppell's, W = lappet-faced, X = white-headed, Y = hooded, Z = Egyptian. Data are from Appendix T.

African white-backed vultures are most generalized in feeding, as indicated by the widest niche breadth (Table 5.1). The most similarity, as measured by the largest niche overlap, is between Rüppell's and lappet-faced vultures (Table 5.2). The mathematical results for each axis are in Appendix U.

Niche metrics of the second analysis (that of scavenging carcasses from varied sources) show that African white-backed vultures are most generalized, as indicated by the widest niche breadth (Table 5.1). The most similarity, as measured by the largest niche overlap, is between African white-backed and Rüppell's vultures (Table 5.2). The mathematical results are in Appendix U.

Comparisons are made of the 4 out of 10 niche axes where statistically significant differences exist. White-backed and Rüppell's vultures appear consistently most similar in their scavenging behavior. The results for each axis are:

Axis I comprises the times of day when vultures were present at carcasses. The test result shows no statistically significant difference in the occurrence of the vultures among the times of day ($X^2 = 1.07$, df = 2, $p < 0.70$, two-tailed).

Axes II through V comprise the physiognomic vegetation types, weather, occurrence of other scavenging birds, and occurrence of Carnivora. On each of these axes the test criteria of minimum expected cell frequencies cannot be met.

Axis VI comprises the time of arrival of vultures at a carcass. The test result shows no statistically significant difference in the occurrence of the vultures among the times of day ($X^2 = 0.69$, df = 2, $p < 0.80$, two-tailed).

Table 5.1 Niche breadth relationships year-round among all six species of vulture, calculated by three methods. Species are listed in order of decreasing non-circular niche breadth. The three methods of calculation are used on the data in Appendix T; the mathematical results are in Table U.1 of Appendix U. Abbreviations: U = African white-backed, V = Rüppell's, W = lappet-faced, X = white-headed, Y = hooded, Z = Egyptian.

Relative Niche Breadth	Axes I to VI			Axes I to X		
	Product Method	Summation Method	Projection Method	Product Method	Summation Method	Projection Method
Widest breadth	U	U	U	U	U	X
	W	W	W	W	W	W
	V	V	V	X	X	Z
	Y	Y	Y	V	V	Y
	X	X	X	Y	Y	V
Narrowest breadth	Z	Z	Z	Z	Z	U

Table 5.2 Niche overlap relationships year-round among all six species of vulture, calculated by three methods. Species-pairs are listed in order of decreasing non-circular niche overlaps. The three methods of calculation are used on the data in Appendix T; the mathematical results are in Table U.2 of Appendix U. Abbreviations: U = African white-backed, V = Rüppell's, W = lappet-faced, X = white-headed, Y = hooded, Z = Egyptian.

Relative Niche Overlap	Axes I to VI			Axes I to X		
	Product Method	Summation Method	Projection Method	Product Method	Summation Method	Projection Method
Greatest overlap	VW	VW	UW	UV	UV	YZ
	UW	UW	VW	VW	VW	VW
	UV	UV	UV	UW	UW	UV
	WY	WY	WY	WX	WY	WX
	VY	VY	UY	UX	VY	VX
	UY	UY	VY	WY	UY	UW
	VX	VX	VX	VY	WX	VY
	UX	UX	UX	VX	UX	WY
	WX	WX	WX	UY	VX	VZ
	XY	XY	XY	XY	LY	UY
	UZ	UZ	UZ		UZ	UX
	VZ	WZ	WZ		WZ	XY
	WZ	VZ	YZ		VZ	WZ
Least overlap		YZ	VZ		YZ	XZ
		XZ	XZ		XZ	UZ
Zero overlap	XZ			UZ		
	YZ			VZ		
				WZ		
				XZ		
				YZ		

Axis VII comprises the parts of the carcass that vultures scavenged (Fig. 5.2). The differences in frequency of occurrence of the three kinds of carcass parts eaten by the five vulture species are statistically significant (X^2= 873.91, df = 8, $p < 0.001$, two-tailed).

Axis VIII comprises the sequence of vulture arrivals and departures at carcasses (Fig. 5.3). The differences in frequency of occurrence of the two times of day when six vulture species ate are statistically significant (X^2= 275.15, df = 5, $p < 0.001$, two-tailed).

Axis IX comprises the occurrences of other carnivorous birds, conspecific or otherwise, when the vulture is feeding at a carcass (Fig. 5.4). The differences in frequency of occurrence of the numbers-present categories where six species of vultures ate are statistically significant (X^2= 86.29, df = 10, $p < 0.001$, two-tailed).

Axis X comprises the carcass sizes upon which vultures fed (Fig. 5.5). The differences in frequency of occurrence of the six vulture species at three carcass sizes are statistically significant (X^2= 177.67, df = 10, $p < 0.001$, two-tailed).

5.3 Discussion

As was true of the Carnivora in the preceding chapter, the results of the present chapter provide a picture of which vultures are most generalized or most specialized, and which are most similar in their use of the ungulate food resource. These niche relationships must always be viewed in the context of which food resources and which feeding behaviors are measured.

Ecological differences among the vultures were discussed by Houston (1975a), who concluded that the African white-backed vulture and

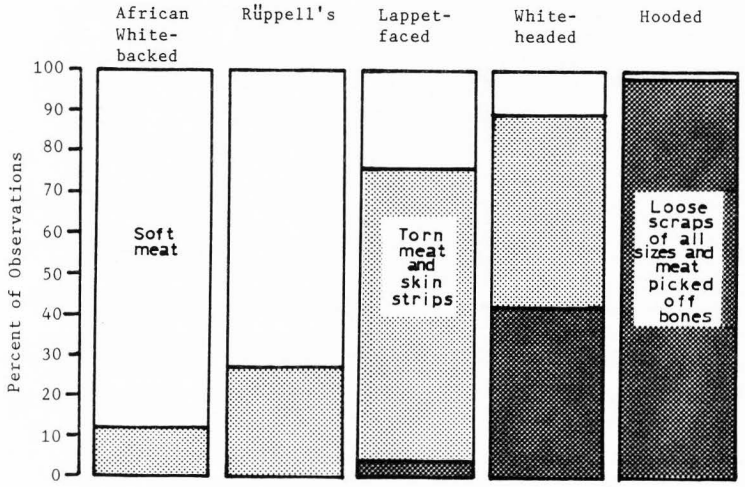


Figure 5.2 Percent frequencies year-round in which five species of vulture fed on three types of carcass parts. Data are from Appendix T.

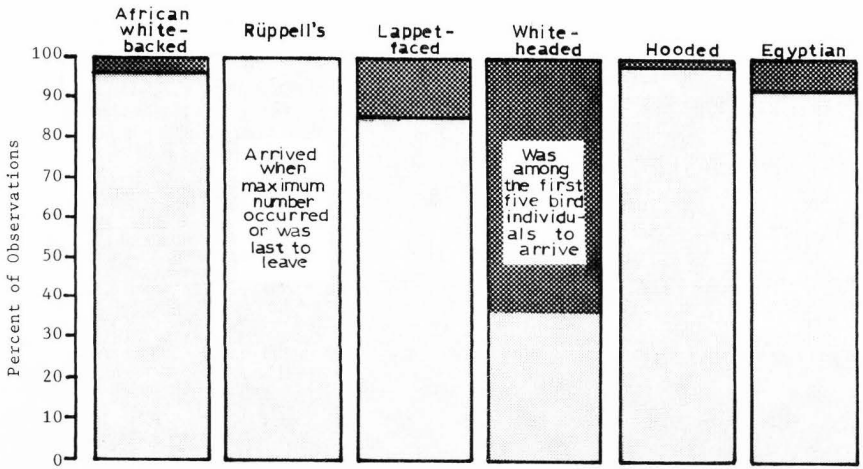


Figure 5.3 Percent frequencies year-round in which six species of vulture occurred in two categories of arrival and departure at carcasses. Data are from Appendix T.

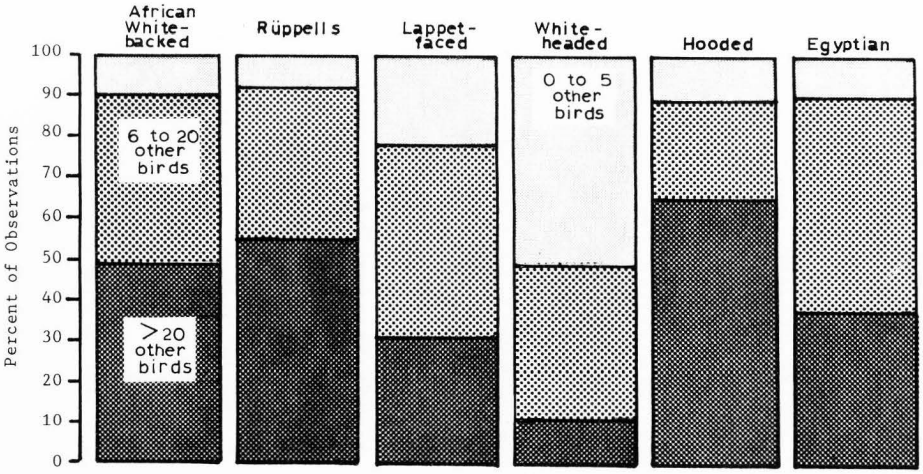


Figure 5.4 Percent frequencies year-round in which six species of vulture fed at a carcass when other carnivorous birds of three group sizes were present. Data are from Appendix T.

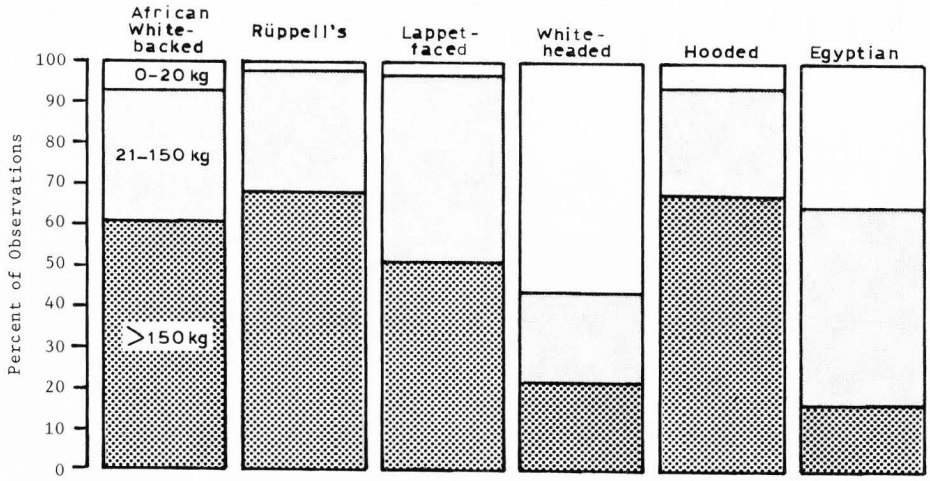


Figure 5.5 Percent frequencies year-round in which six species of vulture fed at three carcass sizes. Data are from Appendix T.

Rüppell's vulture are in direct competition except for some geographical separation. Houston also concluded that Lappet-faced vultures and white-headed vultures feed on different-sized carcasses, and the hooded vulture and the Egyptian vulture are geographically separated.

Examination of carnivorous birds, from the perspective of scavengers on cheetah-killed prey, shows that African white-backed vultures are most generalized year-round throughout the ecosystem (Table 5.1). The lappet-faced vultures rank second (Table 5.1). When compared ecologically and behaviorally, the avian ungulate-eaters show high similarity between Rüppell's and lappet-faced (Fig. 5.1 and Table 5.2), and between African white-backed and Rüppell's (Table 5.2).

The two most-similar vulture dyads, from the cluster and niche analyses, seem to be Rüppell's and lappet-faced, as well as African white-backed and Rüppell's. A high similarity was also shown for African white-backed and Egyptian, but this is probably due to Egyptian vultures being inadequately sampled. African white-backed seems most generalized and Egyptian seems most specialized. The graphs suggest a high similarity between African white-backed and Rüppell's in the types of carcass parts they utilize. And the white-headed is most different from all the other vultures by arriving first and staying only when none or few other vultures are present.

These results support Houston's (1975a) conclusion that African white-backed vultures and Rüppell's vultures are in direct competition, but my analyses further suggest direct competition between lappet-faced vultures and Rüppell's vultures.

CHAPTER VI

RELATIVE ABUNDANCES OF THE FAUNAS

6.1 Identifying Limited Food Resources

I calculate the number of prey animals relative to the number of predators first for the entire Serengeti ecosystem, and then for the study areas by season. Demonstration of a decreased prey:predator ratio in the dry season on the Serengeti Plains is essential to show that intensified competition for limited prey resources is likely at that time of year. And, comparison of the Serengeti Plains and Ngorongoro Crater ratios is expected to show that the latter study area is a stable environment for carnivores, providing a predictable supply of prey and other resources.

Seasonal and locational changes in the prey:predator ratio give a perspective on when interspecific competition is more likely to be severe. This method was used for African fauna by Bourliere (1965), Smuts (1978a), and others (reviewed in Eltringham 1979:182). The intensity of interspecific competition can vary considerably, as was shown among lizards during periods of drought-induced food scarcity versus times of food abundance (Dunham 1980).

6.2 Prey and Predator Densities

Population densities of entire carnivorous and insectivorous mammalian faunas have not previously been estimated for any place in the tropics (Bourliere 1983). The following estimates are made to help

fill this void and to set the background for subsequent discussions of this study.

For the entire 35,500 sq km Serengeti ecosystem (Bradley 1976), densities of both predators and their prey are calculated in two ways. In the first calculation, predators of greatest interest are the five largest mammalian species--lion, spotted hyena, leopard, cheetah, and African wild dog. Their estimated numbers are presented in Table 2.1. The Serengeti ecosystem's year-round density of the five largest predators is 1 per 1.95 sq km (= 0.513/sq km).

The second calculation for predators in the entire Serengeti ecosystem includes all seven ungulate-eating Carnivora. Inclusion of the two jackal species greatly increases the numbers of predators (Table 2.1). The Serengeti ecosystem's year-round density of the seven predators is 1 per 0.646 sq km (= 1.55/sq km).

The third calculation is for the 30 species of the Orders Perissodactyla and Artiodactyla (Appendix A), which are the major prey of the five largest predators. Estimated numbers of these ungulates are presented in Table 2.2. The year-round densities of the 30 prey species in the Serengeti ecosystem is 1 per 0.01179 sq km (= 84.85/sq km).

The fourth calculation is for prey in the entire Serengeti ecosystem. In addition to ungulates, this includes two other prey types--lagomorphs and rodents--which are important foods for jackals. To further generalize, several less-important prey of the large Carnivora also are included. Their estimated numbers are taken from Table 2.2. The Serengeti ecosystem's year-round density of the large and small prey species is 1 per 0.0001957 sq km or 1 per 195.7 sq m

(= 5,110/sq km).

On the Serengeti Plains the wet-season density of predators is 1 per 0.45 sq km (= 2.22/sq km) and the density of prey is 272/sq km (perissodactyls and artiodactyls) or 486/sq km (all the herbivores in Table 2.4).

On the Serengeti Plains the dry-season density of predators is 1 per 1.16 sq km (= 0.86/sq km) and the density of prey is 24/sq km (perissodactyls and artiodactyls) or 88 per sq km (all the herbivores in Table 2.4).

In the Ngorongoro Crater the wet-season density of predators is 1 per 0.36 sq km (= 2.78/sq km) and the density of prey is 90/sq km (perissodactyls and artiodactyls).

In the Ngorongoro Crater there is no detectable seasonal change in predator numbers, and slightly more prey are available in the dry season. The dry-season density of predators is the same as in the wet season, and that of the prey is 102 per sq km (perissodactyls and artiodactyls).

All of these calculations are based on the estimated herbivore and carnivore numbers in 1977. Population data for most of the species are inadequate to assess how the total numbers vary from year to year.

6.3 Prey:Predator Ratios

The ratio of prey numbers to ungulate-eating carnivore numbers for the entire Serengeti ecosystem is calculated in several ways. These ratios provide the first indication of a limitation on the resources that are available. The ratios also facilitate comparisons with ecosystems elsewhere in Africa. In the first calculation, the

predators of greatest interest are the five largest mammalian species that are ungulate-eaters, namely the lion, spotted hyena, cheetah, leopard, and African wild dog. They depend primarily upon 30 species of the mammalian Orders Perissodactyla and Artiodactyla (Appendix A) for satisfying their food requirements. See Tables 2.2 and 2.1 for the estimated numbers of these prey and predators, respectively. The ratio of prey to predators is 165:1.

The second calculation for the entire Serengeti ecosystem includes seven ungulate-eating Carnivora species (two jackal species now included). Prey again comprises the 30 species of perissodactyls and artiodactyls. The estimated numbers of these prey and carnivores again are taken from Tables 2.2 and 2.1, with the calculated prey-to-predator ratio being 55:1.

The third calculation for the entire Serengeti ecosystem again includes all seven ungulate-eating Carnivora species. But now the inclusion of the two jackal species with the five largest carnivores is accompanied by the inclusion of the additional prey types important to them, viz. lagomorphs and rodents. To further generalize, several less-important prey of the lions, spotted hyenas, cheetahs, leopards, and African wild dogs are included. Hence, for these seven predators, all the prey species in Table 2.2 are included. The estimated numbers of these prey and carnivores again are taken from Tables 2.2 and 2.1, with the prey-to-carnivore ratio calculated at 3,303:1

For the central Serengeti Plains in the wet season, all seven species of ungulate-eating Carnivora are compared with the herbivores, as enumerated in Tables 2.3 and 2.4. The ratio of total numbers of perissodactyls and artiodactyls to total numbers of seven Carnivora is

121:1.

For the central Serengeti Plains in the dry season, all seven of the species of ungulate-eating Carnivora are compared with all the herbivores, as enumerated in Tables 2.3 and 2.4. The ratio of total numbers of perissodactyls and artiodactyls to the seven Carnivora is 28:1. This represents more than a three-fourths decrease in relative abundance of prey to mammalian carnivores during the dry season, even after 62% of the seven large Carnivora have left the plains with the migratory prey.

For the Ngorongoro Crater in the wet season, all seven Carnivora species that are ungulate-eaters are compared to all perissodactyls and artiodactyls, as enumerated in Tables 2.5 and 2.6. The ratio of prey to predators is 32:1.

For the Ngorongoro Crater in the dry season, all seven ungulate-eating Carnivora are compared to all perissodactyls and artiodactyls, as enumerated in Tables 2.5 and 2.6. The ratio of prey to predators is 37:1.

These ratios are discussed further in the next section, where they are compared to ratios elsewhere in Africa.

6.4 Comparisons With Other Ecosystems

The total numbers of the Serengeti ecosystem's 30 species of perissodactyl and artiodactyl prey, compared with the total numbers of the five largest ungulate-eating Carnivora, gives the ratio of 161:1 in the referent year 1977 (Tables 2.1 and 2.2, and Section 6.3). Including the populations of the two jackal species reduces the ratio to 55:1. If the populations of the additional prey species of the

jackals are included, the prey-to-predator ratio becomes 3,303:1. Of the three ratios, the first (165:1) probably is the most reasonable to compare to the ratios of a decade earlier.

In the 1960's, the reported prey-to-predator ratios were 397 to 477:1 in the Serengeti National Park and 338:1 in the Ngorongoro Crater (Schaller 1972, cited in Eltringham 1979:182). Another estimate was 250 to 300:1 in the Serengeti National Park and 100:1 in Ngorongoro Crater (Schaller 1972, cited in Berry 1981). This apparent change in ratio through time suggests a proportionately larger increase in predator populations compared to the increase in prey populations. There is so much variability in methodology, however, that the apparent change in ratios could be an artifact.

A wide range of prey:predator ratios have been reported from eastern and southern Africa. At Lake Manyara National Park, Tanzania, a ratio of 70:1 exists (Schaller 1972), or 174:1 (Schaller 1972, cited in Berry 1981). At Nairobi National Park, Kenya, the ratio in 1961 was 260:1, when the prey population was larger and the lion population was about the same as in later years (Eltringham 1979:182). Nairobi Park in 1966 and 1976 had ratios ranging between 159:1 and 152:1, omitting ostriches and giraffes (Foster and Kearney 1967; Foster and McLaughlin 1968). Another estimate in Nairobi National Park is 100:1 (Schaller 1972, cited in Berry 1981). In Kruger National Park the ratio is 100:1 (Pienaar 1969, cited in Berry 1981). In Etosha National Park it is 72 to 105:1 (Berry 1981). The 165:1 ratio in the Serengeti ecosystem in 1977 is similar to that in Nairobi National Park around the same time.

Some authors have considered ratios of prey to lions only. For 1977, my estimated ratio of the total numbers of the Serengeti

ecosystem's 30 species of perissodactyl and artiodactyl prey compared with the total numbers of lions is 948:1. Tarangire National Park, Tanzania, was reported to have an ungulate-prey-to-lion ratio of 292:1, and Ngorongoro Crater at that time had a ratio of 260:1 (Lamprey 1962, cited in Bourliere 1965). The ungulate-to-lion ratio reported in Kagera National Park, Rwanda, was 300:1, and in Virunga National Park, Zaire, excluding elephants and hippos, was 360:1 (Bourliere 1965). Kruger National Park, R.S.A., has a prey-to-lion ratio of 249:1 (Eltringham 1979:182). The Central District of Kruger Park has a large-and-medium-sized ungulates-to-lions ratio of 110:1 (Smuts 1978a). Other prey-to-lion ratios reported from Kruger National Park are 100 to 116:1 (Smuts 1976b, cited in Berry 1981) and 57 to 149:1 (Smuts 1978c, cited in Berry 1981). In Etosha National Park, Namibia, the ratio is 107 to 153:1 (Berry 1981). My estimated ratio of 948:1 for the Serengeti lions is high, probably, in part, because I included more ungulate species. Lions have social constraints on their own density (Bertram 1973; Starfield et al. 1981), so it seems unlikely that the lower ratios elsewhere are due to greater densities of lions. The difference suggests that the Serengeti's lions do indeed have a relatively great abundance of prey compared to the other parks.

The ratios of prey to large carnivores, and of prey to lions, indicate that the Serengeti ecosystem is not unusual in its proportions of prey and predators. Where the Serengeti appears to differ, however, is in having a relatively larger proportion of other large carnivores, particularly the spotted hyena. Whether this difference is real, or merely a result of inaccurate population estimates, is unclear.

CHAPTER VII

INTERSPECIFIC SEASONAL NICHES

7.1 Similarities Change in an Unpredictable Environment

I hypothesize that ther are important seasonal differences in the niche similarities of the larger Carnivora on the Serengeti Plains, due to the unpredictability of the environment. The rainfall is temporally and spatially erratic, causing the larger herbivores to move unpredictably on a local scale (cf. Sections 2.1 and 2.4; also, see L. Pennycuick 1975; Norton-Griffiths et al. 1975). Thus, the wet season is a time of certainty for the carnivores, and the dry season is a time of uncertainty. The niche occupied by a carnivore on the plains must vary as the carnivore responds to changes in resource availability, interactions with competitors and predators, and other influences.

Although the niche descriptions in Chapter Five show which carnivores are most alike in their use of foods, time, and space, the similar use of resources in itself does not constitute exploitation competition. The comparison by season helps to identify which resources might be limiting, and which of the Carnivora are likely to be competing. Carnivora that are most similar during the dry season, are the species that are likely to be competing most intensely.

Carnivore niches in the wet season (November to May) and in the dry season (June to October) are examined in five comparisons, using the Serengeti Plains data. The resource use data are from my field

research in 1972-78 and from several published sources (cf. Appendix C).

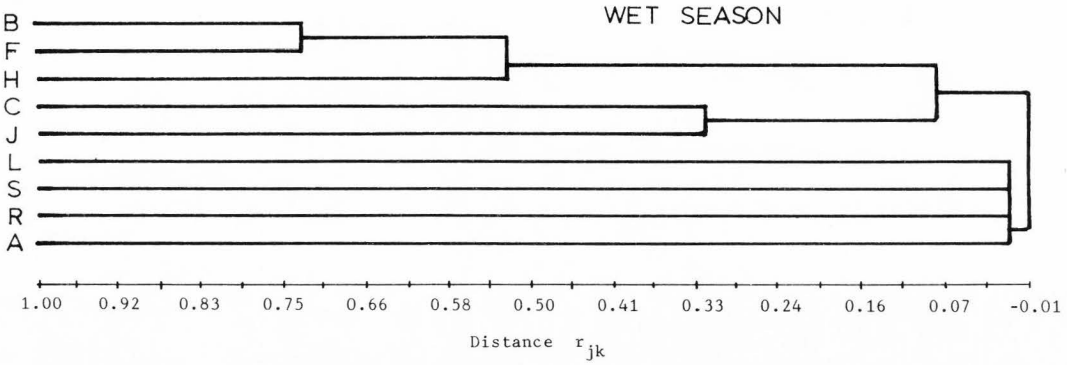
7.2 Nine Carnivora

Nine species of Carnivora--lion, spotted hyena, cheetah, black-backed jackal, common jackal, side-striped jackal, aardwolf, ratel, and bat-eared fox--were recorded within the wet-season and dry-season survey transects on the Serengeti Plains in 1977. The number of observations of each species is presented in Appendix E, where 35 transects provide the wet-season totals and 37 transects provide the dry-season totals. Unlike the analysis in Section 4.2, the data here are combined only by season.

Through cluster analysis of the nine Carnivora (Fig. 7.1), black-backed jackals and bat-eared foxes are most similar in their wet-season occurrence among the survey transects on the Serengeti Plains. Spotted hyenas are the next most similar predator. In the dry season the spotted hyenas and side-striped jackals are most similar, and no other predator is very similar to them. The resemblance matrix and cophenetic correlation for both seasons are given in Tables I.6 and I.7 (Appendix I).

Non-circular niche metrics show that in the wet season spotted hyenas are most ubiquitous in their occurrence on the Serengeti Plains, as indicated by the widest niche breadth (Table 7.1). Spotted hyenas and common jackals are most similar in their occurrence, as indicated by the largest wet-season niche overlap. In the dry season, spotted hyenas again are most ubiquitous in their occurrence, as indicated by the widest niche breadth (Table 7.2). Cheetahs and black-backed

Figure 7.1 Dendrograms of nine Carnivora, showing similarity in wet-season and dry-season occurrence among survey transects on the Serengeti Plains. Abbreviations: L = lion, H = spotted hyena, C = cheetah, B = black-backed jackal, J = common jackal, S = side-striped jackal, A = aardwolf, R = ratel, F = bat-eared fox. Data are from Appendix E.


WET SEASON
B
F
H
C
J
L
S
R
A
1.00 0.92 0.83 0.75 0.66 0.58 0.50 0.41 0.33 0.24 0.16 0.07 -0.01
Distance r_{jk}

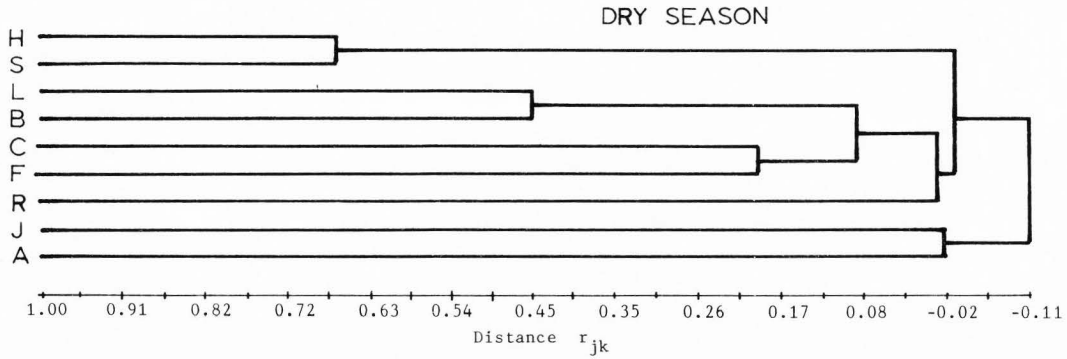

DRY SEASON
H
S
L
B
C
F
R
J
A
1.00 0.91 0.82 0.72 0.63 0.54 0.45 0.35 0.26 0.17 0.08 -0.02 -0.11
Distance r_{jk}

Table 7.1 Niche breadths and niche overlaps in the wet season among nine Carnivora. Measurement is by their occurrence while observers drove along transects. Abbreviations: H = spotted hyena, C = cheetah, B = black-backed jackal, J = common jackal, S = side-striped jackal, A = aardwolf, R = ratel, F = bat-eared fox.

Carnivora Species	Niche Breadth	Pairwise Niche Overlaps							
		H	C	B	J	S	A	R	F
Lion	.32	.58	.05	.46	.44	.00	.00	.00	.47
Spotted Hyena	.64		.05	.72	.79	.00	.00	.00	.57
Cheetah	.17			.35	.53	.00	.00	.00	.00
Black-backed jackal	.47				.55	.00	.00	.00	.74
Common jackal	.50					.00	.00	.00	.23
Side-striped jackal	.00						.00	.00	.00
Aardwolf	.00							.00	.00
Ratel	.00								.00
Bat-eared fox	.25								

Table 7.2 Niche breadths and niche overlaps in the dry season among nine Carnivora. Measurement is by their occurrence while observers drove along transects. Abbreviations: H = spotted hyena, C = cheetah, B = black-backed jackal, J = common jackal, S = side-striped jackal, A = aardwolf, R = ratel, F = bat-eared fox.

Carnivora Species	Niche Breadth	Pairwise Niche Overlaps							
		H	C	B	J	S	A	R	F
Lion	.12	.00	.29	.31	.00	.00	.00	.00	.30
Spotted hyena	.35		.27	.27	.37	.09	.02	.02	.00
Cheetah	.24			.59	.00	.00	.00	.00	.44
Black-backed jackal	.30				.13	.00	.00	.02	.28
Common jackal	.29					.15	.04	.04	.00
Side-striped jackal	.07						.00	.00	.00
Aardwolf	.00							.00	.00
Ratel	.01								.00
Bat-eared fox	.13								

jackals are most similar in their occurrence, as indicated by the largest dry-season overlap.

Comparison suggests that lions and spotted hyenas are most similar in showing the greatest seasonal fluctuation in their use of the Serengeti Plains. The percent frequencies with which the six carnivores were observed in each season are:

Lions 87% wet season, 13% dry season;

Spotted hyenas 80% wet season, 20% dry season;

Cheetahs 75% wet season, 25% dry season;

Black-backed jackals 70% wet season, 30% dry season;

Common jackals 59% wet season, 41% dry season;

Bat-eared foxes 76% wet season, 28% dry season.

The differences in the frequencies of occurrence with which lions, spotted hyenas, cheetahs, black-backed jackals, common jackals, and bat-eared foxes occurred seasonally on the Serengeti Plains ($X^2 = 32.53$, $df = 5$, $p < 0.001$, two-tailed).

7.3 Lion, Spotted Hyena, Cheetah, and African Wild Dog

All the sightings of these four Carnivora during seven months of the hare sampling are tallied by season in this analysis. While driving in search of hares, I recorded every sighting of lions, spotted hyenas, cheetahs, and African wild dogs both inside and outside the transects. There were 429 transects during the wet season and 574 transects during the dry season, although not all were associated with sightings of Carnivora. The resource categories are described in Section 4.5. The analyses include 11 niche axes with a total of 40 occupied resource states in the wet season and 37 in the dry season

(Appendix M).

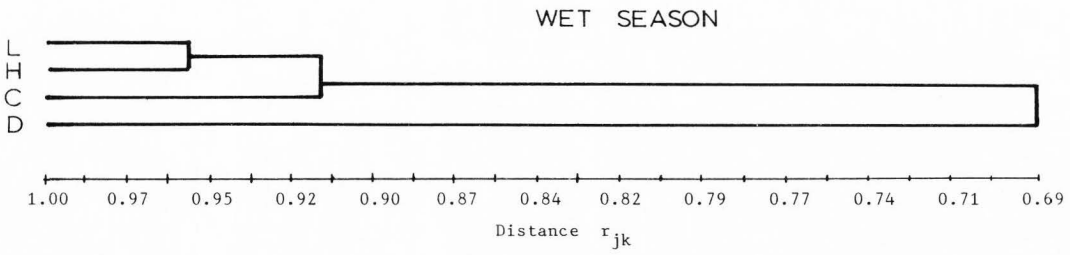
By cluster analysis, using only the marginal totals (cf. Section 3.2.b), lions and spotted hyenas are most similar during the wet season (Fig. 7.2). In the dry season lions and cheetahs are most similar. The resemblance matrix and cophenetic correlation for the two seasons are given in Tables I.8 and I.9 (Appendix I).

Non-circular niche metrics show that in the wet season spotted hyenas and cheetahs are tied for being the most generalized, as indicated by the widest niche breadth (Table 7.3). Lions and spotted hyenas are most similar, as indicated by the largest wet-season niche overlap. In the dry season spotted hyenas are the generalists, as indicated by the widest niche breadth (Table 7.4). Lions and cheetahs are tied with lions and spotted hyenas in being the most similar, as indicated by the largest dry-season niche overlap. Mathematical results for each axis, calculated in three ways, are in Appendix V.

Comparisons are made of the 4 out of 11 niche axes where statistically significant differences exist. In the graphs lions and spotted hyenas appear most similar in the wet season, but spotted hyenas tend to be more similar to cheetahs in the dry season. The Carnivora are included separately for the wet season and dry season. In most comparisons, however, an inadequate sample size necessitates omitting African wild dogs from the comparison, and some resource categories must be combined. The results of each axis are:

Axis I comprises the time of day when carnivores were sighted. Test results show no statistically significant differences in the occurrence of four carnivores by season between two times of day ($X^2 = 10.24$, $df = 5$, $p < 0.10$, two-tailed).

Figure 7.2 Dendrograms of lion, spotted hyena, cheetah, and African wild dog, showing similarity in wet-season and dry-season occurrence in 40 resource states on 11 niche axes. Computed from marginal totals. Abbreviations: L = lion, H = spotted hyena, C = cheetah, D = African wild dog. Data are from Appendix M.


WET SEASON
J
H
C
D
1.00 0.97 0.95 0.92 0.90 0.87 0.84 0.82 0.79 0.77 0.74 0.71 0.69
Distance r_{jk}

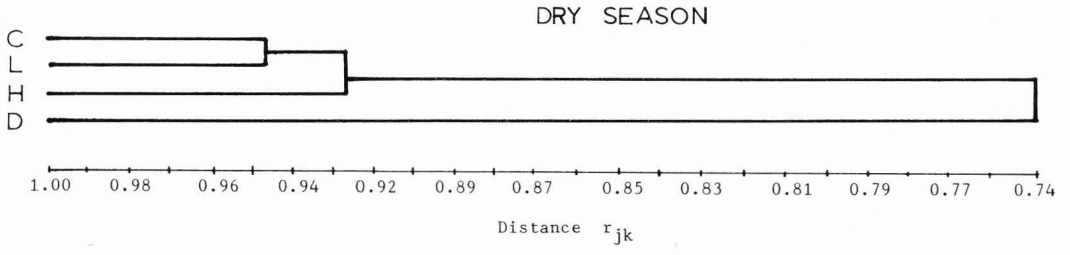

DRY SEASON
C
J
H
D
1.00 0.98 0.96 0.94 0.92 0.89 0.87 0.85 0.83 0.81 0.79 0.77 0.74
Distance r_{jk}

Table 7.3 Niche-breadth relationships in the wet and dry seasons among lion, spotted hyena, cheetah, and African wild dog, calculated by three methods. Species are listed in order of decreasing non-circular niche breadth. The three methods of calculation are used on the data in Appendix M; the mathematical results are in Table V.1 of Appendix V. Abbreviations: L = lion, H = spotted hyena, C = cheetah, D = African wild dog.

Relative Niche Breadth	Wet Season			Dry Season		
	Product Method	Summation Method	Projection Method	Product Method	Summation Method	Projection Method
Widest breadth	H	H	C	H	H	H
	L	C	H		C	C
	C	L	L		L	L
Narrowest breadth		D	D		D	D
Zero breadth	D			L		
				C		
				D		

Table 7.4 Niche-overlap relationships in the wet and dry seasons among lion, spotted hyena, cheetah, and African wild dog, calculated by three methods. The species pairs are listed in order of decreasing non-circular niche overlap. The three methods of calculation are used on the data in Appendix M; the mathematical results are in Table V.2 of Appendix V. Abbreviations: L = lion, H = spotted hyena, C = cheetah, D = African wild dog.

Relative Niche Breadth	Wet Season			Dry Season		
	Product Method	Summation Method	Projection Method	Product Method	Summation Method	Projection Method
Greatest overlap	LH	LH	LH		LH	LC
	LC	LC	HC		LC	HC
		HC	LC		HC	LH
		LD	LD		CD	LD
		CD	HD		HD	CD
Least overlap		HD	CD		LD	HD
Zero overlap	LD			LH		
	HC			LC		
	HD			LD		
	CD			HC		
				HD		
				CD		

Axis II comprises the vegetative cover where carnivores were sighted (Fig. 7.3). The two habitat cover categories are: None/slight/moderate cover (all short grasslands and medium grasslands with or without herbs or shrubs) and dense/tall cover (woodlands or riverine forests or thickets on kopjes). The differences in frequency of occurrence of lions, spotted hyenas, and cheetahs by season among the two cover densities are statistically significant ($X^2 = 25.68$, $df = 5$, $p < 0.001$, two-tailed).

Axes III through V comprise weather, the occurrence of moonlight, and greenness of the grassland where the carnivores were sighted. On each of these axes the test criteria of minimum expected cell frequencies was not met.

Axis VI comprises the occurrence of water on the plains where the carnivores were sighted (Fig. 7.4). The differences in frequency of occurrence of lions, spotted hyenas, and cheetahs by season among the three water-availability categories are statistically significant ($X^2 = 200.58$, $df = 10$, $p < 0.001$, two-tailed).

Axis VII comprises the availability of Thomson's gazelles where the carnivores were sighted (Fig. 7.5). The differences in frequency of occurrence of lions, spotted hyenas, and cheetahs by season among the three gazelle-availability categories are statistically significant ($X^2 = 68.69$, $df = 10$, $p < 0.001$, two-tailed).

Axis VIII comprises the availability of wildebeest where the carnivores were sighted (Fig. 7.6). The differences in frequency of occurrence of lions, spotted hyenas, and cheetahs by season among the three wildebeest-availability categories are statistically significant ($X^2 = 270.12$, $df = 10$, $p < 0.001$, two-tailed).

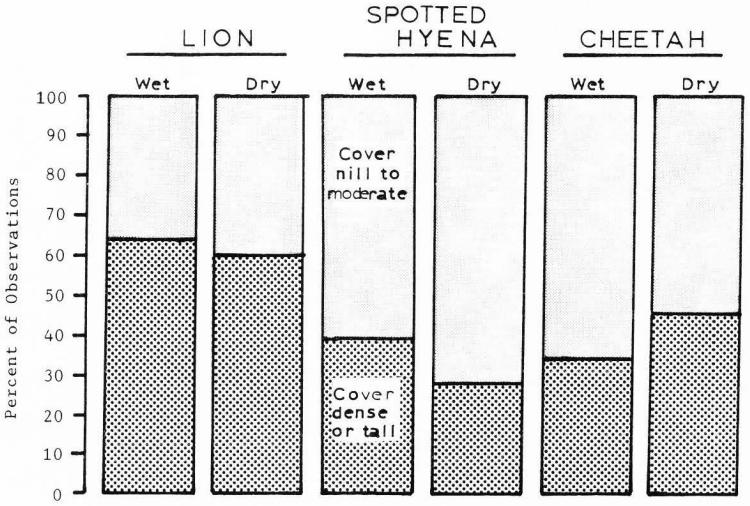


Figure 7.3 Percent frequencies in the wet and dry seasons in which lion, spotted hyena, and cheetah were seen in two densities of vegetative cover. Data are from Appendix M.

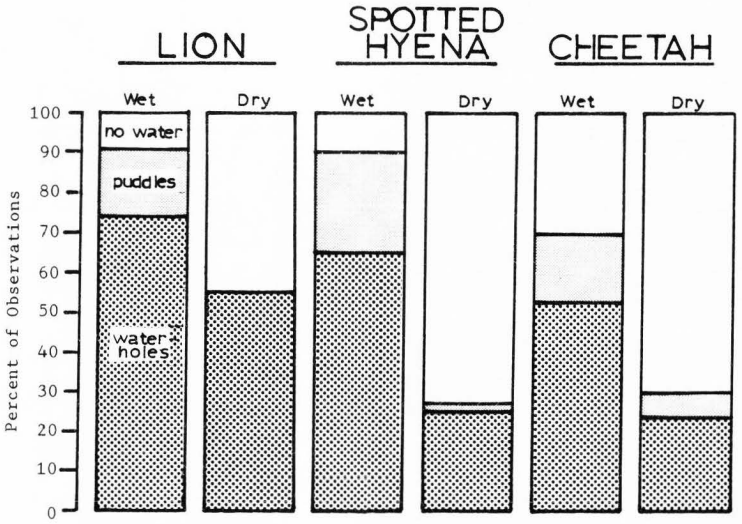


Figure 7.4 Percent frequencies in the wet and dry seasons in which lion, spotted hyena, and cheetah were seen in areas of three availabilities of water. Data are from Appendix M.

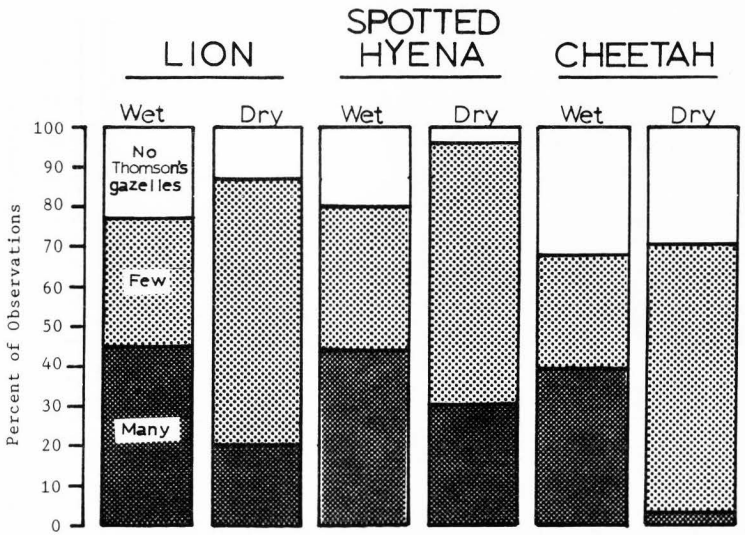


Figure 7.5 Percent frequencies in the wet and dry seasons in which lion, spotted hyena, and cheetah were seen in areas of three availabilities of Thomson's gazelle. Data are from Appendix M.

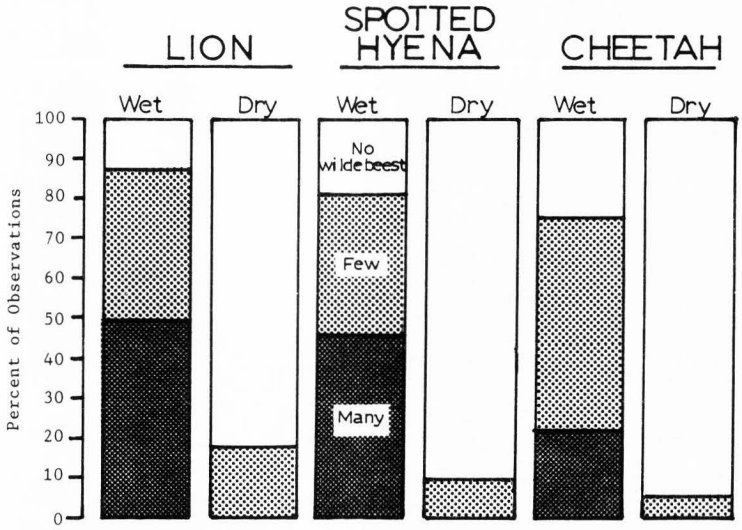


Figure 7.6 Percent frequencies in the wet and dry seasons in which lion, spotted hyena, and cheetah were seen in areas of three availabilities of wildebeest. Data are from Appendix M.

Axis IX comprises the availability of hares where the carnivores were sighted. The test criteria of minimum expected cell frequencies cannot be met.

Axes X and XI comprise the presence or absence of ostriches and warthogs as indices of the occurrence of carnivores. The test results show no statistically significant difference in the occurrence of lions, spotted hyenas, and cheetahs by season for the ostrich ($X^2 = 2.48$, df = 5, $p < 0.80$, two-tailed) and warthog ($X^2 = 8.45$, df = 5, $p < 0.20$, two-tailed) categories of occurrence.

7.4 Lion, Cheetah, and African Wild Dog

This comparison addresses the seasonal shift in use of the migratory prey--zebra, wildebeest, and Thomson's gazelle--by lions, cheetahs, and African wild dogs. The lion data of migratory prey killed are from Schaller (1972). The migratory prey species caught or scavenged by cheetahs and African wild dogs in the wet and dry seasons are from the field studies of G.W. Frame and L.H. Frame (unpubl. data). The data for all three Carnivora are in Appendix O.

No cluster analysis was performed, because only three species are being compared.

Circular niche metrics are calculated for lion, cheetah, and African wild dog. Niche breadths in the wet season are 0.96 for lion, 0.61 for cheetah, and 0.32 for African wild dog. In the dry season they are 0.78 for lion, 0.12 for cheetah, and 0.36 for African wild dog. Niche overlaps in the wet season are 0.90 for lion and cheetah, 0.61 for lion and African wild dog, and 0.85 for cheetah and African wild dog. In the dry season the overlaps are 0.62, 0.73, and 0.85,

respectively.

Graphical comparison of lions, cheetahs, and African wild dogs shows that all shifted to more Thomson's gazelles in their diets in the dry season (Fig. 7.7). The seasonal differences in the frequency of occurrence of the three migratory prey species in the diets of lions, cheetahs, and African wild dogs are statistically significant ($X^2 = 250.90$, df = 10, $p < 0.001$, two-tailed).

7.5 Cheetah and African Wild Dog

I compared all prey species, migratory and non-migratory, that were hunted or scavenged by cheetahs and African wild dogs. They represent 18 species, or occupied resource states, in the wet season and 13 in the dry season. The data are listed in Appendix O, and are taken from the field studies of G.W. Frame and L.H. Frame (in prep.) and L.H. and G.W. Frame, unpubl. data).

By circular niche metrics for cheetah and African wild dog, cheetahs are the relative generalists in hunting behavior and ecology in both seasons. The wet-season circular niche breadths are 0.68 for cheetahs and 0.24 for wild dogs, and their circular niche overlap is 0.71. The dry-season circular niche breadths are 0.59 for cheetahs and 0.38 for wild dogs, and their circular niche overlap is 0.54.

From the graph of foods eaten (Fig 7.8), cheetahs and African wild dogs appear more similar during the dry season than in the wet season. Seasonal differences in the frequency of occurrence of five food types in the diets of cheetahs and African wild dogs are statistically significant ($X^2 = 144.44$, df = 12, $p < 0.001$, two-tailed). The food types are large ungulates (buffalo, zebra, wildebeest), medium

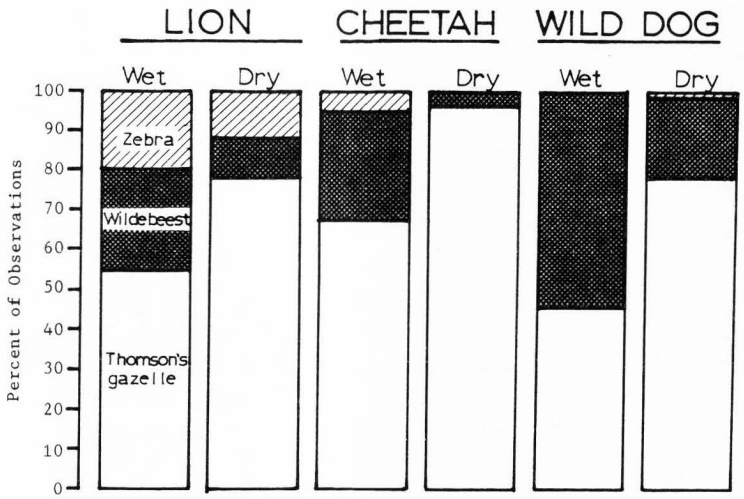


Figure 7.7 Percent frequencies in the wet and dry seasons in which lion, cheetah, and African wild dog hunted or ate the migratory zebra, wildebeest, and Thomson's gazelle. Data are from Appendix O.

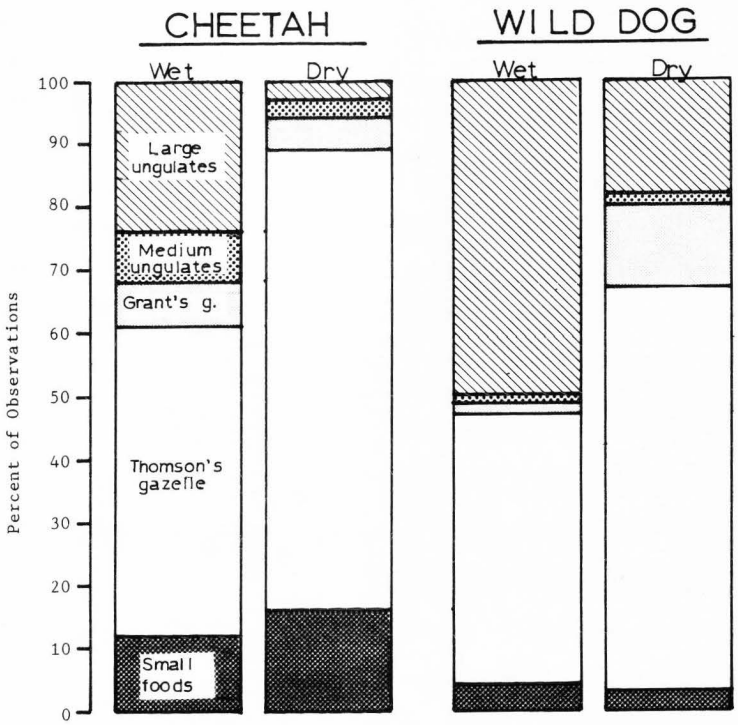


Figure 7.8 Percent frequencies in the wet and dry seasons in which cheetah and African wild dog hunted or ate five food types. Data are from Appendix O.

ungulates (kongoni, topi, impala, reedbuck), Grant's gazelle, Thomson's gazelle, and small mammals and other foods (warthog, dik dik, springhare, hare, common jackal, birds, beetles, termites, grasses, cardboard).

7.6 Black-backed Jackal and Common Jackal

Black-backed jackals were compared with common jackals using data from Lamprecht (1978a), described here in Section 4.8. The count data, calculated from Lamprecht's percentages, are listed in Appendix S.

By circular niche metrics of black-backed jackal and common jackal, neither is more of a generalist in the wet season, their food habits being very similar then. But, in the dry season, the common jackal is considerably more of a generalist than is the black-backed jackal, their food habits being very different then. The wet-season niche breadths are 0.57 for black-backed jackal and 0.58 for common jackal, and their overlap is 0.90. The dry-season niche breadths are 0.23 for black-backed jackal and 0.80 for common jackal, and their overlap is 0.19.

From the graph of foods eaten (Fig. 7.9), black-backed jackals and common jackals appear more similar in their diets during the wet season than in the dry season. Seasonal differences in the frequency of occurrence of four food types in the diets of the two jackal species are statistically significant ($X^2 = 35.89$, $df = 9$, $p < 0.001$, two-tailed). The four food categories are ungulates, small mammals and birds, arthropods, and vegetable matter or trash.

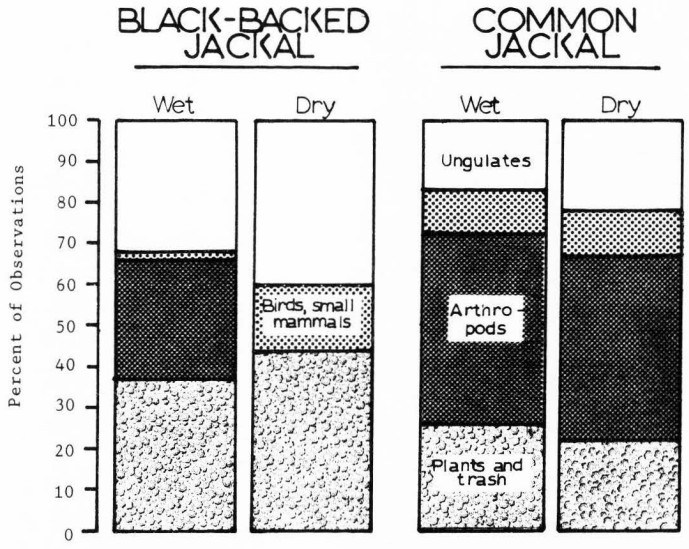


Figure 7.9 Percent frequencies in the wet and dry seasons in which black-backed jackal and common jackal ate four food types. Data are from Appendix S.

7.7 Discussion

The results of this chapter provide specific examples of how the Carnivora differ in their use of resources on the Serengeti Plains during the predictable conditions of the wet season compared with the unpredictable dry season. Both interference competition and exploitation competition are more likely to occur during the dry season, when there are localized food shortages.

Among the six ungulate-eating Carnivora that were recorded in survey transects, the lions, spotted hyenas, black-backed jackals, common jackals, and bat-eared foxes have less-generalized distributions in the dry season. In contrast, cheetahs appear to have a more-generalized distribution in the dry season, although the difference is not large enough to be confident that it is real. This suggests that in the dry season, most large Carnivora either abandon large portions of the plains or else are more inclined to stay hidden during the daytime when the surveys were carried out.

The sightings of Carnivora during hare surveys suggest that lions, cheetahs, and African wild dogs have a more restricted distribution among the less-varied ecological conditions of the dry season. The spotted hyenas in contrast seem to be less affected.

Lions, cheetahs, and African wild dogs have more similarity in their diets in the dry season compared with the wet season. The measure was their use of migratory prey.

When only cheetahs and African wild dogs are examined in greater detail, they appear to diverge further in their hunting behavior and

ecology in the dry season. As measured by hunting behavior and ecology, cheetahs are more specialized in the dry season, and African wild dogs are more specialized in the wet season.

Black-backed jackals and common jackals diverge further in their food habits during the dry season. Black-backed jackals are more specialized in the wet season.

In summary, there is increased potential for exploitation competition in the dry season when there are fewer prey per predator on the Serengeti Plains. The ungulate-eating Carnivora appear to avoid unfavorable localities as far as is possible within the constraints of territoriality and site attachment. Thus, they seldom experience prolonged depletion of critical responses. All the Carnivora considered seem to have substantial differences in their food habits at all times of the year. The seasonal niches are discussed further in Chapter Fourteen.

CHAPTER VIII

INTERSPECIFIC LOCATIONAL NICHES

8.1 Similarities Change in a Varying Environment

I hypothesize that ungulate-eating Carnivora differ in their resource use on the Serengeti Plains compared with the Ngorongoro Crater. This essentially is a comparison between the varying environment of the plains and the stable environment of the caldera. The distinction made in Chapter Seven was between the dry season and wet season on the Serengeti Plains, where the unpredictability of the of the dry-season rain showers--that is, if and when they occur, week by week--makes finding food uncertain for the ungulate-eaters. In the present chapter the time perspective is shifted to an annual scale. The Serengeti Plains has a varying prey environment, with the migratory ungulates predictably arriving and departing in an annual cycle. In contrast, the Ngorongoro Crater has a stable prey environment, i.e. the ungulate populations are essentially resident (cf. Section 2.4). Both locations have the same resources available--prey, water, cover--but these are dependably abundant year-round only for the Carnivora in the caldera. It is likely, therefore, that high similarity in resource use among Carnivora dyads on the Serengeti Plains is more indicative of competition than it is at Ngorongoro Crater.

I examined Carnivora niches in four comparisons of foods eaten in these two locations. The Carnivora that are compared are chosen because they appear to provide meaningful comparisons, and because

adequate data for them are available. The resource-use data are from my 1972-78 field research and from published sources (cf. Appendix C).

8.2 Seven Carnivora

The resource states considered are the foods eaten by lions, spotted hyenas, leopards, cheetahs, African wild dogs, black-backed jackals, and common jackals. The foods recorded as eaten, their frequencies, and the sources of these data are listed separately for the Serengeti Plains and woodlands (Appendix W) and the Ngorongoro Crater and adjacent forests (Appendix X). The two appendices contain the same data that are in earlier Appendices, plus additional data from other cited sources, all tallied by location. In the Serengeti data there are 83 occupied resource states containing a total of 3,506 observations. In the Ngorongoro Crater data there are 40 states, containing 542 observations.

By cluster analysis of the seven Carnivora on the Serengeti Plains, leopards and cheetahs are most similar in the prey species they ate (Fig. 8.1). No other predator is very similar to them. Lions and spotted hyenas are two other highly similar predators on the Serengeti Plains. In the Ngorongoro Crater, lions and spotted hyenas are most similar in the prey species they ate. Black-backed jackals are the next most similar predator in the caldera. The resemblance matrix and cophenetic correlation for the two locations are given in Tables I.10 and I.11 (Appendix I).

Non-circular metrics for the Serengeti Plains show that black-backed jackals are generalists, as measured by the widest niche breadth (Table 8.1). Lions and spotted hyenas are most similar, being

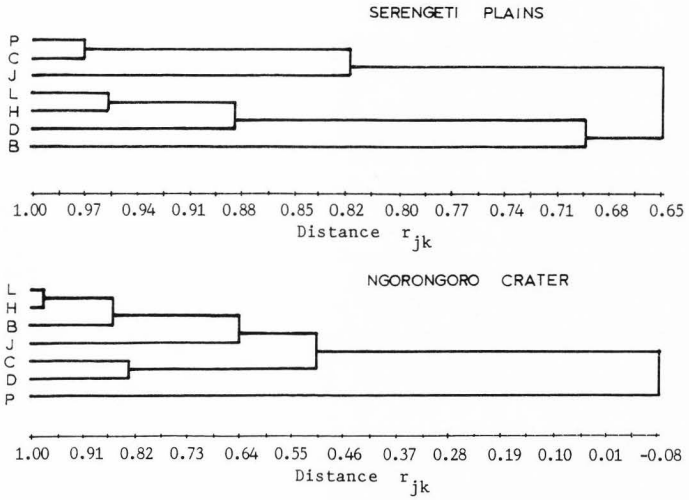


Figure 8.1 Dendrograms of seven Carnivora, showing similarity at the Serengeti Plains and Ngorongoro Crater locations in the use of 83 prey species and food types. Abbreviations: L = lion, H = spotted hyena, C = cheetah, P = leopard, D = African wild dog, B = black-backed jackal, J = common jackal. Data are from Appendices W and X.

Table 8.1 Niche breadths and niche overlaps at the Serengeti Plains location among seven Carnivora. Abbreviations same as Figure 8.1.

Carnivora Species	Niche Breadths	Pairwise Niche Overlaps					
		H	C	P	D	B	J
Lion	.39	.99	.70	.77	.94	.89	.82
Spotted hyena	.36		.70	.80	.93	.88	.83
Cheetah	.15			.97	.82	.64	.81
Leopard	.27				.91	.71	.90
African wild dog	.31					.83	.87
Black-backed jackal	.58						.90
Common jackal	.45						

Table 8.2 Niche breadths and niche overlaps at the Ngorongoro Crater location among seven Carnivora. Abbreviations same as Figure 8.1.

Carnivora Species	Niche Breadths	Pairwise Niche Overlaps					
		H	C	P	D	B	J
Lion	.30	.95	.45	.01	.91	.93	.85
Spotted hyena	.20		.14	.04	.85	.85	.71
Cheetah	.14			.00	.59	.56	.72
Leopard	.04				.03	.00	.00
African wild dog	.20					.85	.82
Black-backed jackal	.38						.97
Common jackal	.46						

nearly identical in their diets, as indicated by the largest niche overlap on the plains. For the Ngorongoro Crater, common jackals are the generalists, as measured by the widest niche breadth (Table 8.2). Black-backed jackals and common jackals are most similar in their diets, as indicated by the largest niche overlap in the caldera.

The graphs show a greater use of wildebeest in the Ngorongoro Crater, with lions and spotted hyenas being very similar (Figs. 8.2 and 8.3). There also is a greater similarity between African wild dogs and black-backed jackals in the caldera. Differences in the frequency of occurrence of five food types in the diets of the seven Carnivora species in two locations are statistically significant ($X^2 = 2,097.51$, $df = 48$, $p < 0.001$, two-tailed). It was, however, necessary to delete cheetahs in Ngorongoro Crater, because of the small sample size. The food types are: (1) zebras, (2) wildebeest, (3) Thomson's gazelles, (4) other large and medium ungulates (elephants, giraffes, buffalos, eland, waterbuck, kongoni, topi, impala, bushbuck, reedbuck, Grant's gazelles, domestic donkeys, domestic cattle, domestic goats), and (5) small ungulates or smaller foods (i.e. everything else listed in Appendices W and X).

8.3 Five Largest Carnivora

The prey species and food types of Appendices W and X are used again, but the two jackal species are omitted to get better discrimination among the five larger Carnivora. In the Serengeti Plains and woodlands data, there are 57 occupied resource states containing a total of 3,376 observations, and in the Ngorongoro Crater and adjacent forests data there are 31 states containing 494

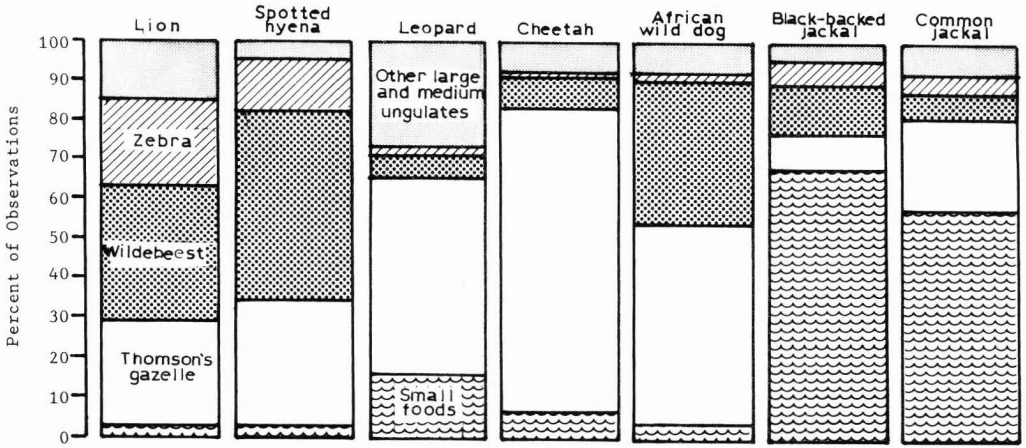


Figure 8.2 Percent frequencies at the Serengeti location in which seven Carnivora hunted or ate five food types. Data are from Appendices W and X.

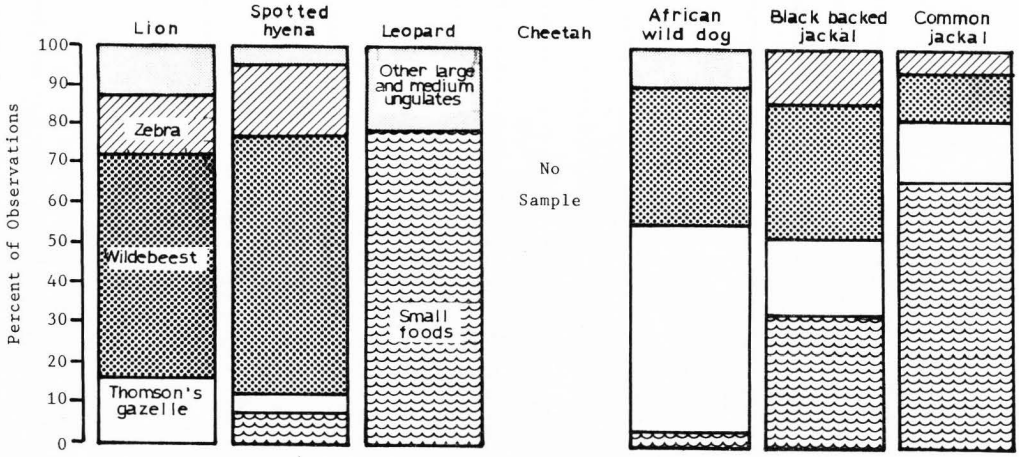


Figure 8.3 Percent frequencies at the Ngorongoro Crater location in which six Carnivora hunted or ate five food types. Data are from Appendices W and X.

observations.

Comparisons of the five largest Carnivora show through cluster analyses that on the Serengeti Plains the cheetahs and leopards are most similar in the prey species they ate (Fig. 8.4). No other predator is very similar to them. In the Ngorongoro Crater the lions and spotted hyenas are most similar in the prey species they ate, and no other predator is very similar to them. The resemblance matrix and cophenetic correlation for each location is given in Tables I.12 and I.13 (Appendix I).

Non-circular niche metrics for the Serengeti Plains (Table 8.3) and Ngorongoro Crater (Table 8.4) show that lions are relative generalists in their food habits in both locations, as measured by the widest niche breadth. Lions and spotted hyenas in both locations are nearly identical in their food habits, as indicated by their very large niche overlap.

If both jackals in Figures 8.2 and 8.3 are ignored, the differences in the frequency of occurrence of five food types in the diets of lions, spotted hyenas, cheetahs, leopards, and African wild dogs in two locations are statistically significant (X^2= 1,381.99, df = 32, $p < 0.001$, two-tailed). Cheetahs in the Ngorongoro Crater are deleted because of their small sample size.

8.4 Lion, Spotted Hyena, and African Wild Dog

Again the prey species and food types of Appendices W and X are used, but this time only lion, spotted hyena, and African wild dog are considered, to get better discrimination among them. In the Serengeti Plains and woodlands data there are 39 occupied resource states,

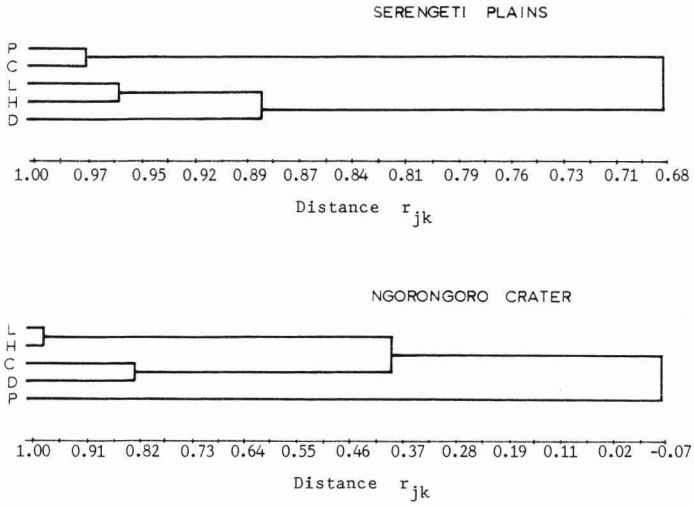


Figure 8.4 Dendrograms of five Carnivora, showing similarity at the Serengeti Plains and Ngorongoro Crater locations in the use of 57 prey species and food types. Abbreviations: L = lion, H = spotted hyena, C = cheetah, P = leopard, D = African wild dog. Data are from Appendices W and X.

Table 8.3 Niche breadths and niche overlaps at the Serengeti Plains location among the five largest Carnivora. Abbreviations in Fig. 8.4.

Carnivora Species	Niche Breadths	Pairwise Niche Overlaps			
		H	C	P	D
Lion	.51	.99	.71	.76	.94
Spotted hyena	.46		.70	.80	.93
Cheetah	.18			.97	.83
Leopard	.36				.91
African wild dog	.40				

Table 8.4 Niche breadths and niche overlaps at the Ngorongoro Crater location among the five largest Carnivora. Abbreviations in Fig. 8.4.

Carnivora Species	Niche Breadths	Pairwise Niche Overlaps			
		H	C	P	D
Lion	.40	.95	.53	.01	.91
Spotted hyena	.26		.17	.05	.82
Cheetah	.21			.00	.67
Leopard	.04				.02
African wild dog	.23				

containing a total of 2,614 observations. And in the Ngorongoro Crater and adjacent forests data, there are 26 states containing 474 observations.

Circular niche metrics are calculated. In the Serengeti location the niche breadths are: lion 0.63, spotted hyena 0.48, and African wild dog 0.27. The niche overlaps are: lion and spotted hyena 0.95, spotted hyena and African wild dog 0.85, and lion and African wild dog 0.71. In the Ngorongoro location the niche breadths are: lion 0.58, spotted hyena 0.37, and African wild dog 0.48. The niche overlaps are: lion and spotted hyena 0.90, lion and African wild dog 0.84, and spotted hyena and African wild dog 0.60.

Only these three Carnivora are now considered in the graphs (Figs 8.2 and 8.3). Differences in the frequency of occurrence of five food types in the diets of lions, spotted hyenas, and African wild dogs in two locations are statistically significant ($X^2 = 489.61$, df = 20, $p < 0.001$, two-tailed).

8.5 Black-backed Jackal and Common Jackal

Finally, only black-backed Jackals and common jackals are compared, using their prey species and food types of Appendices W and X. In the Serengeti Plains and woodlands data there are 43 occupied resource states containing a total of 130 observations. And in the Ngorongoro Crater and adjacent forests data there are 19 states containing 48 observations.

Circular niche metrics are calculated. Niche breadths in the Serengeti location are 0.48 for black-backed jackal and 0.30 for common jackal, with a niche overlap of 0.74. In the Ngorongoro

location niche breadths are 0.24 for black-backed jackal and 0.83 for common jackal, with an overlap of 0.70.

Only the two jackals are now considered in the graphs (Figs. 8.2 and 8.3). Differences in the frequency of occurrence of three food types in the diets of the two jackals in two locations are statistically significant ($X^2 = 10.76$, $df = 6$, $p < 0.10$, two-tailed).

8.6 Discussion

This chapter provides specific examples of how the Carnivora differ in their use of prey species and other food types between the unpredictable environment of the Serengeti Plains and the predictable environment of the Ngorongoro Crater. On the plains the larger ungulates are nomadic, which results in the predators and scavengers experiencing frequent food shortages. At such times these carnivores must switch to other foods or travel in search of the ungulates. In the Ngorongoro Crater, by contrast, most ungulates are very localized in their movements, so carnivores can expect the prey always to be available. The same prey species live on the Serengeti Plains and woodland edge as live in the Ngorongoro Crater and forested rim. The only difference is that on the caldera floor, impala and giraffes are absent, and warthogs are rare or sometimes absent.

Niche breadth, as measured by the foods eaten, generally appears to be narrower for lions, spotted hyenas, cheetahs, leopards, African wild dogs, and black-backed jackals at the Ngorongoro location. The common jackal food-niche breadth was slightly larger, probably negligibly so, at Ngorongoro Crater. Leopards seem to have the greatest difference in diet between the two locations, apparently lacking close contact with

zebras, wildebeest, and Thomson's gazelles in the Ngorongoro area and substituting smaller prey there. Lions and spotted hyenas, however, eat more of the larger prey in the Ngorongoro location than they do in the Serengeti location.

In conclusion, the ungulate-eating Carnivora appear to have smaller food niches in the predictable environment of Ngorongoro Crater. Locational niches are discussed further in Chapters Twelve and Fourteen.

CHAPTER IX

COMPETITIVE EXCLUSION

9.1 A Non-evolutionary Response to Competition

According to the competitive exclusion hypothesis, two ecologically identical species cannot live together in the same place for any length of time if resources are limited. Competitive exclusion between similar kinds of animals was described by Darwin in 1859 (Hardin 1960:1295), and the phenomenon was subsequently explained by Grinnell in 1904 (cited in Udvardy 1959) and Petersen in 1915 (cited in Svardson 1949:157).

The formal mathematical basis of competition theory, of which the competitive exclusion hypothesis is a part, began with equations proposed independently in the 1920's by Lotka (1932) and Volterra (1926), and subsequently tested by Gause (1934).

Modern competition theory is based on several assumptions, four of which are (Wiens 1977): continuous and intense selection, populations in equilibrium, competition as the major selective force, and availability of the predicted optimal state. These assumptions rarely, if ever, are met in real situations, so the applicability of the competitive exclusion concept to real-life situations is questionable. The remaining paragraphs in this section review some of the previous work, and set the background for evaluating whether or not there is evidence of competitive exclusion in the Serengeti ecosystem.

The main types of evidence supporting the competitive exclusion hypothesis were reviewed by Orians and Collier (1963), who added their

own observations of interactions between two species of blackbirds. In one field study, removal of one vole species resulted in another vole species moving into the vacant habitat (Koplin and Hoffmann 1968). And when several species of parasitic Hymenoptera were introduced successively into an area, they competed for the same host species until only one predator remained (Varley et al. 1973:33-34).

Competitive exclusion occurs only when populations approach resource limitation and undergo high levels of interspecific competition (Cody 1974:213-214). Critically limited resources sometimes are other than food or space, and they can be of low intensity (Huffaker and Laing 1972). A study of leafhopping insects (Erythroneura spp.) concluded that in the absence of interspecific competition there apparently is no predictable limit to the number of species that can occupy the same niche (Ross 1957:128). Without competition, a species is versatile and utilizes many resources.

Although simple removal experiments demonstrate the effect of one species on another, they do not reveal the actual mechanism of the competition (Schoener 1974b). However, it was found during a study of intertidal predatory sea stars (Paine 1966) that the number of prey species declined when one or more predator species was removed. The explanation given was that predation prevents competitive exclusion.

The Volterra model has had its critics (Gilbert et al. 1952; Andrewartha and Birch 1954; Cole 1960; O.L. Smith et al. 1975), and alternatives have been proposed (Herbert et al. 1956; Ayala 1969; O.L. Smith et al. 1975). Armstrong and McGehee (1980) suggest that the competitive exclusion principle is applicable in a general way only to coexistence when densities are fixed, because that situation does not

require the assumption of linearity in per capita growth rate of the species. Problems with the theory resulting from the assumption of equilibrium were discussed by Levins (1979), who concluded that coexistence is possible without stable equilibrium. According to Tilman (1980), an unlimited number of species can coexist stably in a spatially heterogeneous environment--even if they are competing for essential resources. Limit cycles in competition systems were discussed by Gilpin (1975). R. Levins (1968) extended the Volterra competition equations to include any number of coexisting species.

Some studies found the competitive exclusion hypothesis to be inadequate (e.g. Gilbert et al. 1952; O.L. Smith et al. 1975). A different model, which relates the concentration of limiting environmental resources to the specific growth rate, was described as being an improvement (Herbert et al. 1956; Waldon 1975). The case of many competing species in a community was discussed by Vandermeer (1970). Critical review of the recent models of MacArthur and Levins (1967), Roughgarden (1974), and Cody (1974) suggests that progress in understanding resource partitioning probably requires more-detailed models of specific systems (Abrams 1975:372).

An attempt to invalidate the competitive exclusion hypothesis met with apparent success (Ayala 1969). However, experimental conditions are crucial in determining which population replaces the other (Park 1954). Critiques of Ayala's methods and logic (Ito 1971; Gilpin and Justice 1972; Varley et al. 1973:42-43) render his experiment inconclusive. The supposed invalidation was criticized by Gause (1970) as being in no way a test of the hypothesis, because the two species in Ayala's experiment clearly had different niches. The real points of

dispute lie partly in the definitions of competition and ecological niche (Ayala 1970). Actually, the Lotka-Volterra equations do not deal in niches per se, but instead describe the impacts of the species on each other (Frederic H. Wagner, pers. comm.).

The competitive-exclusion hypothesis, when expressed in a biologically meaningful way, is not testable (Birch and Ehrlich 1967). Even closely related species, when coexisting, utilize resources in slightly different ways (e.g. R.S. Miller 1964; Rosenzweig 1973). Two organisms are never exactly alike; therefore, they cannot have the same potential niche. Further experimentation by Ayala (1971) led to the conclusion that two competing species can indeed coexist in stable equilibrium--if their relative fitnesses are frequency dependent, i.e. fitnesses must be inversely related to numbers.

When the assumption that the effects of intraspecific and interspecific competition are proportional to population density is not met in experiments, coexistence occurs (Varley et al. 1973:33). Identical competitors probably could coexist if an external factor interceded, or if the environmental variables oscillated so as to continually reverse the direction of competition (Hutchinson 1948). In competitive interactions between a generalist and a specialist, the specialist is predicted to be the winner (Morse 1974; Colwell and Fuentes 1975:291-292). The primary cause of competitive exclusion probably is not the extent of niche similarity that exists, but instead the lack of niche diversification with regard to requirements that are in limited supply (King 1964:716).

The degree of tolerable overlap in resource use needs to be focused on (Cody 1974:54). The question should not be why the competitive

exclusion hypothesis so rarely, if ever, applies, but how overlap in resource use varies with changing availabilities of the resources. Numerous attempts have been made to identify guilds that persist in apparent contradiction to the competitive exclusion hypothesis, but eventually most have been shown to differ in some other niche dimension or not to meet the assumption of equilibrium (Cody 1974:210). Two very similar species, one model predicts, will continue to converge until one eventually becomes extinct (MacArthur and Levins 1967; MacArthur 1972). This is an exception to the general rule that two species competing for resources will be under selective pressure to maintain and increase the differences in their patterns of resource utilization. The probability of convergence is considered extremely unlikely (Lawlor and Smith 1976).

When there are competing species, each withdraws to utilize the resources for which it is best adapted (Dobzhansky 1950). In a field situation, mink and otters in Britain showed some dietary overlap, but seemed not to be in competition, because food was abundant (Wise et al. 1981:210). Their densities in Sweden, however, seemed to be inversely related, which led Erlinge (1972) to conclude that food competition in winter apparently restricted otter to optimal habitats, fitting the included niche model of Hutchinson (1957) and R.S. Miller (1967). The ultimate effect of competitive exclusion is one population producing enough individuals to cause the disappearance of the other population. Or, in a sense, the proximate effect is a dominant organism preventing another organism from utilizing a resource.

In spite of the experimental problems, the competitive-exclusion phenomenon sometimes occurs in nature, especially under limited

conditions such as with cultivated plants or with animals living in a stable environment in which the amount of food available is critical in sustaining population density (Ito 1971). Perhaps its acceptance as theory should be defended in the same way as Ferguson (1976) did for the theory of evolution.

The development of the competitive exclusion concept since early in this century is reviewed by Armstrong and McGehee (1980), Jackson (1981), and Schoener (1982). Competitive exclusion among species is rare in nature, and when species do compete, the effects usually are moderated by chance, weather, predators, and pathogens (Simberloff 1982). Observational evidence in support of competitive exclusion is less than had been thought earlier (Strong 1980; Schoener 1982), and the coexistence of so many carnivores in the Serengeti begs an answer.

9.2 The Evidence

We might not expect competitive exclusion to occur on the Serengeti Plains, because the carnivores all differ in some important niche dimensions, while prey numbers and kinds vary and are unpredictable. However, one apparent case of impending competitive exclusion among the Carnivora is shown by a decline of African wild dogs in the presence of increased numbers of spotted hyenas on the Serengeti Plains. Second and third possible examples of competitive exclusion are the near absence of African wild dogs and cheetahs in the Ngorongoro Crater, a location where spotted hyenas and lions predominate. There is no evidence that any of the other large Carnivora are sensitive to competitive exclusion.

9.2.a African Wild Dog

The first example is the best documented. Early in the study of African wild dogs on the Serengeti Plains, L. Herbison Frame and I found, upon comparing our data with those collected earlier by J.R. Malcolm (pers. comm.), that the plains population of wild dogs was substantially smaller than it had been several years earlier. The number of packs on the Serengeti Plains declined from 12 to 7 from 1970 to 1977, with a corresponding decrease in the number of individuals from 95 to 26 (L.H. Frame et al. 1979). The prey species were increasing in abundance during this period (Norton-Griffiths 1972; Sinclair and Norton-Griffiths 1982), which left the following three likely explanations for the decline of wild dogs: shooting, disease, and competitive exclusion. Wild dogs were shot on the plains until the end of 1973 (T. Mcharo, pers. comm.). There was evidence that disease, possibly canine distemper, killed some wild dogs on the plains (Schaller 1972; G. and L. Frame 1981; L.H. Frame 1985a). And wild dogs often were seen competing with spotted hyenas for food at the dogs' kills (Estes and Goddard 1967; G. and L. Frame 1981). All three of these hypotheses were addressed by trying to identify the causes of wild dog deaths. Much pup mortality resulted from predation by spotted hyenas and combined disease and starvation at a time when spotted hyenas were appropriating prey from those packs (L.H. and G.W. Frame, unpubl. data).

The condition which precipitated the decline of the African wild dog population was a succession of years, 1972-76, in which there was

an increased amount of rainfall during the dry season on the Serengeti Plains (Hanby and Bygott 1979:259). The wetter dry seasons allowed more prey to remain on the plains throughout the year. Two surveys (Serengeti Research Institute 1977a; 1977b) showed that the spotted hyena population probably increased in size since a decade earlier (Kruuk 1972a), and that in 1977 a larger number stayed on the Serengeti Plains throughout the dry season. More spotted hyenas resident on the Serengeti Plains in the dry season meant more competition and interaction with the wild dogs at the critical time of year.

Beginning around 1978, the dry-season rainfall decreased on the Serengeti Plains (Patricia Moehlman, pers. comm.), and since then the wild dog population has increased. In early 1985, at least five groups were known; their sizes were 45, 37, 16, 7, and 3, giving a total of 108 wild dogs on the Serengeti Plains (Tim Caro, pers. comm.). It remains to be shown whether there has been a decrease in spotted hyena use of the Serengeti Plains in the dry season since 1978.

The second example is with African wild dogs in the Ngorongoro Crater. A breeding pack resided inside the caldera during part of 1964 and 1965 (Estes and Goddard 1967), and I observed them for several months in 1966. I saw that they were harassed by spotted hyenas, which often appropriated the wild dogs' kills. Estes and Goddard (1967) reported the same kinds of interactions, and considered the spotted hyenas to be serious competitors. Thereafter the wild dogs departed, and for several years there were no wild dogs inside Ngorongoro Crater. Then, in 1973, two wild dogs entered the caldera, but did not stay (Hans Kruuk, pers. comm.; and my unpublished observations). No other wild dogs have been reported within Ngorongoro Crater since 1973,

although they occasionally are seen in the surrounding highlands.

The density of spotted hyenas inside Ngorongoro Crater is 1.85/sq km, calculated from Table 2.5. This is greater than on the Serengeti Plains, where the spotted hyena density is 1.13/sq km in the wet season and 0.28/sq km in the dry season, calculated from Table 2.3. Spotted hyenas, even at that low density, have been observed in the dry season to be devastating competitors for food, as well as predators of wild dog pups (G. and L. Frame 1981). Furthermore, the prey:predator ratio on the Serengeti Plains in the dry season is about the same as inside the Ngorongoro Crater year-round, viz. 28:1 compared to 32:1 respectively (cf. Section 6.3). So, spotted hyenas probably are competitively excluding African wild dogs inside Ngorongoro Crater.

9.2.b Cheetah

The third possible example is with cheetahs in the Ngorongoro Crater. Cheetahs generally were considered to be rare, with the most optimistic estimates by Hendrichs (1970) and Schaller (1972:296) being 200 to 500 cheetahs living in the entire Serengeti ecosystem. My estimate is 1,000 cheetahs in 1977 (G.W. Frame and L.H. Frame, in prep.). The different estimates for cheetahs are a result of the intensities of the studies, and do not show a change in the population. Elsewhere in Africa, cheetahs appear to be competitively excluded by spotted hyenas and African lions (McLaughlin 1970; Eaton 1974). If the densities of lions and spotted hyenas are greater in the Ngorongoro Crater than they are on the Serengeti Plains, I hypothesized that there would be a lower density or absence (except for occasional transients) of cheetahs in Ngorongoro because of competitive exclusion. The

Serengeti Plains densities, calculated from Table 2.3, are the following: In the wet season, lions = 0.22/sq km, spotted hyenas = 1.13/sq km, and cheetahs = 0.08/sq km. In the dry season, lions = 0.03/sq km, spotted hyenas = 0.28/sq km, and cheetahs = 0.03/sq km. The Ngorongoro Crater densities, calculated from Table 2.5 are the following: lions = 0.38/sq km, spotted hyenas = 1.85/sq km, and cheetahs = 0.03/sq km. The few cheetahs that I did see inside the Ngorongoro Crater tended to stay in areas of substantial cover, such as medium grasslands and the forest edge, perhaps to avoid being seen and harassed by the lions and spotted hyenas. The densities of lions and spotted hyenas are indeed greater in Ngorongoro Crater than in either season on the Serengeti Plains. Surprisingly, however, the cheetah density inside the caldera seems to be the same as it is on the Serengeti Plains in the dry season; and cheetahs are doing well in the dry season on the plains (G. Frame and L. Frame, in prep.). The prey:predator ratio is about the same for the dry-season plains as it is in the caldera, so the finding of equal cheetah densities suggests that, contrary to my expectations, there is no evidence of competitive exclusion for this species.

9.3 Discussion

From demographic and behavioral evidence, spotted hyenas appear to competitively exclude the African wild dogs on the Serengeti Plains, as well as in Ngorongoro Crater. The wild dog population on the Serengeti Plains decreased at the same time that spotted hyena numbers increased, and there was a shift in spotted hyena resource use at a critical time of year. In Ngorongoro Crater the absence of African wild dogs is

puzzling except when viewed in the context of the very high spotted hyena density.

The cheetah data, contrary to expectation, did not provide any evidence of competitive exclusion in the Ngorongoro Crater. Despite substantial interference competition and predation from lions and spotted hyenas on the Serengeti Plains (cf. Section 10.2) as well as the similarities in resource use (Chapters Four, Five, Seven, and Eight), there was no reason even to suggest competitive exclusion at that location. The cheetahs are maintaining their numbers in the Serengeti ecosystem. The large proportion of young adults suggests that the population might even be increasing (G.W. Frame and L.H. Frame, in prep.). The greater year-round availability of prey in the drier portions of the ecosystem, and the decreased occurrence of dry-season burning, which kills small cubs and deprives cubs and adults of cover (G.W. Frame and L.H. Frame, in prep.), together might more than compensate for the costs of increased competition.

The competitive exclusion hypothesis seems to apply to some degree in the Serengeti ecosystem wherever spotted hyenas and African wild dogs use the same resource, but complete exclusion seldom occurs. The competitive exclusion concept seems to have widespread applicability, but often defies explanation, in the same way that E.S. Reed (1981) described the natural-selection concept.

In the Serengeti ecosystem, the critical resource is food, and it often is limited only in the sense that it sometimes is very costly, i.e. it requires a large expenditure of energy and increased risk to find and to catch. For the spotted hyenas, it is apparently more efficient for some individuals to appropriate food from African wild

dogs (L.H. and G.W. Frame, unpubl. data), which are highly conspicuous hunters, than to chase the prey themselves.

In conclusion, competitive exclusion, as an extreme population effect, occurs only very locally, e.g. inside the Ngorongoro Crater, where spotted hyenas apparently exclude African wild dogs. The commonly-occurring population phenomenon among the Serengeti's carnivores appears to be that of suppression, rather than exclusion. Suppression and other population effects are discussed further in Section 14.1.

CHAPTER X

SERENGETI CARNIVORES IN COMPETITION

10.1 Competition Causes Aggression

My working hypothesis is that if resource competition exists among the Serengeti's carnivores, then interference competition should be a result, because all aggression is caused by competition for resources (cf. Marler 1976). Interference competition is the result of resources--such as space, food, and habitat--being in short supply. As such, it is an indirect consequence of exploitation competition.

I review the Serengeti carnivore literature in this chapter to show the extent of competition (defined in Section 1.3) among and within the ungulate-eating species. Examples of cleptoparasitism and the killing of other carnivores are described to establish the existence of interference competition.

10.2 Interspecific Interactions

Of the Serengeti ecosystem's numerous examples of interspecific aggression among individuals of the ungulate-eating carnivores, many instances clearly are interference competition for food or other resources, and some might be considered predation. The proximate result of most of these encounters is loss of food, loss of offspring, injury, or even death to the adults. Whether or not the victim is eaten makes little or no difference, because the result is the same--a real or potential competitor is eliminated. The potential competitors

are the ungulate-eaters (cf. Section 2.2). Although interference interactions occur among individuals, a high frequency or strong intensity results in population effects. The interactions among individuals are reviewed below:

10.2.a Lion

Spotted hyenas sometimes chase lions away from kills (Kruuk 1972a:137). Schaller (1972:273) reported that at night on the Serengeti Plains and woodland edge, spotted hyenas took 44% of the carcasses that engorged lions were guarding. In Ngorongoro Crater, about one-third of the prey that were seen killed by lions were eaten by spotted hyenas, either by scavenging after the lions finished (thereby depriving the lions of a second meal) or by driving off the female lions and cubs (Elliott and Cowan 1978). Lions sometimes are mobbed by spotted hyenas. Kruuk (pers. comm., cited in Schaller 1972:274) described an instance of 20 hyenas attacking and chasing two lionesses up trees, and Schaller (1972:274) on three occasions saw spotted hyenas mob a lone lion. Spotted hyenas kill and eat lion cubs (Schaller 1972:428; Bertram 1978:88), but whether or not this is predation depends upon the initial reason for the killing.

A leopard scavenged from a carcass that was temporarily left unattended by a lioness, and the same leopard killed one of that lion's cubs (Schaller 1972:145, 428). Bertram (1978:88, 222; 1982) saw a leopard eating a lion cub.

Black-backed jackals and common jackals often scavenge from lion kills, and generally are ignored by lions (Schaller 1972:274). Lions often lose some of their food to these two jackals, which dart in and

steal scraps; both species have a very short flight distance from lions (Kruuk 1972a:142). Schaller (1972:350) once saw black-backed, common, and side-striped jackals scavenging from the same lion kill.

Vultures harass lions, particularly when the kill is large and it takes several days to eat (Wright 1960). Hooded vultures are often the first vulture species to land where lions are eating, and, because they are small and agile, these birds can pick up scraps of food without being caught by lions (Schaller 1972:274). Schaller (1972:215-216) suggested that lions would not need to kill as often if the abundant African white-backed vultures did not eat so many of the carcasses. Whether or not lion cubs or adults would eat these scraps, even in times of food scarcity, is unclear, but they would return to carcasses.

10.2.b Spotted hyena

Lions are attracted to spotted hyena kills from distances of 3 km or more, and lions even take prey from them before the hyenas have killed it (Kruuk 1972a:134). A few lions can easily take a kill from many spotted hyenas; e.g. one subadult male lion stole a carcass from 17 spotted hyenas, and two lionesses took a carcass from 31 spotted hyenas (Schaller 1972:272). In the Ngorongoro Crater, spotted hyenas lose many of their kills to lions, varying from 10 to 40% (Elliott and Cowan 1978) to as much as 77% (Kruuk 1975a). In the Serengeti Park, lions took 42% of their scavenged meat from spotted hyenas, and in the Ngorongoro Crater they took even more (Schaller 1972:214).

Lions sometimes attack spotted hyenas, even when no food is involved. Schaller (1972:273-274) and Kruuk (1970) described several observations in which lions chased, clawed, and bit spotted hyenas for

no obvious reason. Hyenas are sometimes killed by lions (Kruuk 1972a:135; 1975a:45); of ten killed by them, only one spotted hyena was partially eaten. In a sample of 22 freshly-dead spotted hyenas, 36% were killed by lions (Kruuk 1970). Another instance of a spotted hyena being eaten by lions was reported by Schaller (1972:220). Of the four lion-killed spotted hyenas that Schaller (1972:272) found, only one was beside a carcass. On the rim of Ngorongoro Crater, spotted hyenas tried to chase lions off a zebra kill. In the resulting fight, two spotted hyenas were killed (Cullen 1969:127). In the western Serengeti a lion was seen killing one hyena and stalking two others (Cullen 1969:129).

A leopard killed a spotted hyena cub (Bertram 1982). And a leopard once chased a spotted hyena from the remains of a cheetah-killed gazelle, and the leopard made off with the carcass (S. Downey pers. comm., cited in Kruuk 1972a:138).

African wild dogs caught a half-grown spotted hyena and appeared to be trying to kill it, but other hyenas drove the dogs away (Cullen 1969:132). African wild dogs chased spotted hyenas off kills on five occasions seen by Kruuk (1972a:139; 1975a:41) and one additional time seen by A. Root (pers. comm., cited in Kruuk 1972a:140).

Vultures are very numerous at spotted hyena kills, and eat so much meat that they may force the spotted hyenas to kill more often (Kruuk 1967). Hooded vultures are attracted by the tape-recorded vocalizations of spotted hyenas on a kill (Kruuk 1967). Vultures and spotted hyenas seem to use each other in a relationship of mutual benefit and competition (Kruuk 1972a:145-146).

White-backed vultures and white-headed vultures sometimes are

attracted to spotted hyenas that are hunting, even before they catch any prey (Kruuk 1976).

A crocodile chased ten spotted hyenas away from a wildebeest which the hyenas had killed in a river (Kruuk 1972a:146). The crocodile then ate the carcass.

10.2.c Cheetah

Lions took 12% of their scavenged meat from cheetahs at the woodland edge during the dry season (Schaller 1972:214). Year-round, lions took 20 of 238 kills by cheetahs (Schaller 1972:320). Other records of lions appropriating the kills of cheetahs are in G. and L. Frame (1981:60-61, 69-70, 96, 98, 105, 131-132). Cheetahs do not resist lions other than by vocalizing and lunging at them from a safe distance (Schaller 1972:320). Bertram witnessed two young lionesses killing a cheetah cub, which the mother cheetah did not try to defend (Bertram 1978:176). Bertram (1978:177) reported that these two lionesses were specializing in robbing cheetahs. Lions sometimes kill cheetahs (G. Rilling, pers. comm., cited in G.W. Frame and L.H. Frame, in prep.). An emaciated young adult female cheetah was killed by lions but not eaten (Schaller 1972:220, 302). A cheetah was found dead from a bite through its back. It was next to the remains of a gazelle carcass, and the cheetah's injury suggested that it was attacked by a lion (Cullen 1969:138).

Spotted hyenas require the cheetah to be cautious, although Schaller (1972:320) once saw a cheetah successfully attack and drive off two spotted hyenas, and another time a cheetah hit a spotted hyena in the face as it stole the cheetah's kill. Cheetahs are watched

closely by spotted hyenas which are intent on scavenging the cheetah's food, and they frequently succeed in taking whatever the cheetah has (e.g. G. and L. Frame 1981:9, 12, 97, 101-103, 213). On three occasions observed by Kruuk (1972a:138), cheetahs had their kills taken by a single hyena. Cheetahs in the Serengeti lose 4% of their kills to spotted hyenas (Schaller 1968). Spotted hyenas took 11 of 238 kills by cheetahs (Schaller 1972:320).

A leopard killed and cached a cheetah high in a tree (M. Turner, pers. comm., cited in Schaller 1972:301-302), and this might be the same one that was reported by Kruuk and Turner (1967) and Cullen (1969:137). A leopard killed a cheetah cub (Bertram 1982). Another leopard took one of 238 kills by cheetahs (Schaller 1972:320).

Jackals sometimes follow and bark at cheetahs (Bertram 1978:177). Black-backed jackals seem to follow cheetahs in anticipation of food, and cheetahs sometimes chase them away (cf. G. and L. Frame 1981:12). Two black-backed jackals yapped at cheetahs, apparently to chase the cheetahs from the jackals' territory (G. and L. Frame 1981:15, 16, 212). Jackals that scavenge while a cheetah feeds usually are ignored, but Schaller (1972:320) saw one cheetah chase and swat a jackal.

Vultures, too, usually are ignored while a cheetah eats, but cheetahs sometimes leap and swat at them (Schaller 1972:320). Vultures often take the remains of cheetah kills, and sometimes they seem to drive the cheetahs off before they have finished (G. and L. Frame 1981:67, 69, 70, 97, 99). African white-backed vultures twice drove a cheetah off its prey (Schaller 1972:274, 320). Feeding cheetahs are disrupted by vultures, and the vultures attract lions or spotted hyenas (Bertram 1978:177). Cheetahs sometimes are driven away from their meal

before they finish, but sometimes cheetahs repeatedly rush at vultures (Bertram 1978:177; G.W. Frame and L.H. Frame, in prep.). Of the large predators in the Serengeti, Houston (1974a) concluded that the cheetah probably is the most affected by vultures.

10.2.d Leopard

Lions cause substantial interference competition with leopards (Bertram 1979:223). Lions took 5% of their scavenged meat from leopards (Schaller 1972:214). Bertram (1978:126) saw a male lion climb a tree in an unsuccessful attempt to steal a carcass that a leopard had cached. Schaller (1972:293) reported three instances of lions climbing trees to take a carcass. Two instances of a lion taking a leopard's kill out of a tree were mentioned by Kruuk and Turner (1967), but it is unclear whether or not Schaller (1972:293) counted these records in his total. A lion chasing a leopard shows the same hostile facial expression as when it chases another lion (Bertram 1978:223). Schaller (1972:422) reported five observations of female lions pursuing a leopard up a tree. At the Seronera River, a lion treed a female leopard, and when the leopard tried to come down again she was chased back up, while several lions tore apart the leopard's small cub (Cullen 1969:136). In one instance lions killed a leopard but did not eat it (Schaller 1972:220).

Spotted hyenas, on one occasion one and on another occasion two, chased a solitary leopard from a carcass (Kruuk 1972a:138). The latter probably is the instance recorded in Kruuk and Turner (1967). Adult cheetahs twice were seen chasing a young female leopard up a tree (Bertram 1978:161).

African wild dogs observed by John Pearson (pers. comm.) came upon the scent of a leopard on a kill. The wild dogs chased the leopard, but did not eat the leopard's meal.

Several vultures were seen eating an unattended carcass that a leopard had hung in an acacia tree (Schaller 1972:293).

10.2.e African Wild Dog

Lions take food from wild dogs and sometimes kill them (e.g. see G. and L. Frame 1981:84-85, 88, 109, 224). Lions took 8% of their scavenged meat from wild dogs (Schaller 1972:214). Near Seronera, a pack of wild dogs was killing a topi when a lion chased the dogs away and finished killing the prey (Cullen 1969:139). In a similar incident, a lion caught a wildebeest calf that wild dogs were hunting (G. and L. Frame 1981:109).

Spotted hyenas appropriate much of the dogs' food, particularly in the dry season when food is scarce (cf. G. and L. Frame 1981:41, 72-93, 106-108, 112-113, 151, 160, 198, 206, 217-223). In 37 of 62 wild dog kills observed by Kruuk (1972a:139), hyenas ate at least part of the carcass. In the Ngorongoro Crater, spotted hyenas were serious competitors of wild dogs, sometimes stealing prey even before the dogs finished killing it (Estes and Goddard 1967). When the hyenas arrive early in the hunt, the dogs sometimes attack and bite the hyenas, but seldom injure them (Estes and Goddard 1967; G. and L. Frame 1981). Spotted hyenas also eat wild dog pups (G. and L. Frame 1981:77, 198-199).

A leopard killed an African wild dog pup (Bertram 1982).

Black-backed jackals and common jackals scavenge from African wild

dogs (Estes and Goddard 1967; G. and L. Frame 1981:151).

Vultures often feed at African wild dog kills and at dens, and they sometimes harass the dogs or attract other predators (G. and L. Frame 1981:83, 88, 155). In the Ngorongoro Crater, one of the African wild dogs on a kill repeatedly chased away vultures by jumping up and snapping at them (Cullen 1969:47).

10.2.f Black-backed Jackal

Spotted hyenas take some of the gazelle fawns that black-backed jackals catch (Kruuk 1972a:142-143). In the Serengeti, spotted hyenas appropriated almost 30% of the hares and gazelle fawns caught by black-backed jackals (Lamprecht 1978a).

Cheetahs sometimes chase black-backed jackals, even when no food is involved (G. and L. Frame 1981:209, 212).

A leopard that killed a black-backed jackal for food was reported by Schaller (1972:447), and another example of killing a jackal for food was reported by Kruuk and Turner (1967). Bertram (1982) reported that another leopard killed a black-backed jackal, but he did not indicate whether or not the leopard ate it.

African wild dogs sometimes take kills from black-backed jackals (G. and L. Frame 1981:81-82).

A martial eagle tried to carry away an almost full-grown black-backed jackal, but the jackal escaped when a vulture attacked the eagle (H. and J. van Lawick-Goodall 1970:127-128).

10.2.g Common Jackal

Spotted hyenas take some of the gazelle fawns caught by common

jackals (Kruuk 1972a:142-143). In the Serengeti, spotted hyenas appropriated about 11% of the hares and fawns that common jackals caught (Lamprecht 1978a). A common jackal was chased and killed by a spotted hyena (M. Turner, pers. comm., cited in Kruuk 1972a:143). This probably is the same observation at Barafu Kopjes that was described by Cullen (1969:142). Kruuk (1972a:143) saw spotted hyenas eat a jackal.

A cheetah was seen walking away from the remains of a common jackal on the Serengeti Plains, but whether or not the cheetah killed or ate the jackal in not known (G.W. Frame and L.H. Frame, in prep.).

A leopard killed a common jackal for food (Schaller 1972:447), a clear case of predation.

African wild dogs sometimes take kills from common jackals (G. and L. Frame 1981:111).

An African white-backed vulture joined a common jackal that was catching a gazelle fawn before any blood was shed (Kruuk 1967). Rüppell's vultures try to take food from common jackals (Kruuk 1975a:52).

In some reports, the jackal species was not identified: Lions took 2% of their scavenged meat from jackals (Schaller 1972:214). This apparently refers to the two jackal species combined. A jackal (species not reported) was killed by a lion, but not eaten (Schaller 1972:220, 274). Eleven jackals (species not reported) in the Ngorongoro Crater were caught and eaten by a leopard within a three-week period (R.D. Estes pers. comm., cited in Kruuk and Turner 1967). The relationship between spotted hyenas and the two jackal species was characterized by Kruuk (1972a:143) as being of small mutual benefit, with the two jackals benefiting more than the spotted hyenas. In the Mara portion of the Serengeti ecosystem, two jackals

caught a gazelle fawn which was promptly taken from them by lions (Cullen 1969:141).

When vultures were present at carcasses, single jackals of both species were observed spending most of their time threatening vultures, rather than feeding, and sometimes they were driven away by vultures (Moehlman 1983).

A bateleur eagle carried a 10-week-old common jackal pup into the air, but the pup survived after the eagle dropped it (H. and J. van Lawick-Goodall 1970:127-128). A martial eagle carried away a common jackal pup and the pup did not survive (H. and J. van Lawick-Goodall 1970:127-128).

Tawny eagles commonly steal meat cached by jackals of both species (Lamprecht 1978a).

10.2.h Avian Scavengers

Vultures watch vultures of other species and are attracted when they descend to a carcass (Kruuk 1967).

White-headed vultures are timid and, unlike all the other large scavenging birds in the Serengeti, rarely feed beside other species (Houston 1979). They usually feed alone, eating hares and other small carcasses (they are suspected of killing some of these small prey), and probably are the only species of vulture which gets much of its food from predator kills (Houston 1979). This species seems particularly attracted to spotted hyena kills, and it might follow the movements of the hyenas (Houston 1975a). White-headed vultures represent only 0.3% of the avian scavengers seen at carcasses (Houston 1979).

Lappet-faced vultures are very aggressive. At ungulate carcasses

they usually dominate and drive away Rüppell's vultures and African white-backed vultures (Houston 1979). Lappet-faced vultures represent 8% of the scavenging birds seen at carcasses (Houston 1979).

Rüppell's and African white-backed vultures represent 88% of the scavenging birds seen at carcasses (Houston 1979). These two vultures get most of their food from animals that die of disease or malnutrition, and predator-killed carcasses are relatively unimportant to them (Houston 1975a). They find most of their food by following other vultures and scavenging birds (Houston 1974b). A leopard climbed up to a white-backed vulture nest in an acacia tree along the Seronera River and ate the two chicks (Cullen 1969:48). Two instances in which a white-backed vulture was injured by being bitten or swatted by a lion, and a third case where a lion tried to catch a vulture, were reported by Schaller (1972:274-275).

Scavenging vultures (species not reported) that joined lions at a kill were chased by a lioness, which caught one with her paws; she released the vulture after it pecked her face (Cullen 1969:47). Generally, however, lions ignore vultures if they remain at least 20 m away (Schaller 1972:275). Vultures were chased off carcasses by spotted hyenas (Lamprecht 1978b). Both species of jackals were usually successful in chasing vultures away from a carcass for awhile, but sometimes many vultures together reclaimed the carcass (Lamprecht 1978b). The sight and/or sound of vultures landing causes lions, spotted hyenas, and jackals of both species to come running (Matthews 1939; Kruuk 1967; 1972a). For example, on 11 occasions lions and spotted hyenas were attracted to a feeding cheetah by the descent of vultures (Schaller 1972:320). Of the carcasses scavenged directly by

lions, 11% are the result of watching vultures (Schaller 1972:216).

The two species of vulture which are most aggressive to each other are the African white-backed and the Rüppell's (Kruuk 1975a:58). The frequency of fights observed among vultures of different species was summarized by Kruuk (1967: his Table 2) and Houston (1980: his Table 2).

10.3 Intraspecific Interactions

The Serengeti ecosystem's many examples of aggression within the species of ungulate-eaters are summarized here to describe the existence of intraspecific competition. A review article on intraspecific predation (Polis 1981) documents the prevalence of killing among conspecifics throughout the animal kingdom, although such behavior often is categorized as food-getting.

10.3.a Lion

Rival male lion groups compete intensely in severe, often fatal, fights to possess a pride and its territory (Bertram 1979). After a fight among lions near Seronera, a large male was found with severe bites and was presumed to be dying (Cullen 1969:14). An adult male lion was killed in a fight (Bertram 1978:113). Several examples of aggressive chases among lions in the Serengeti ecosystem were reported by Cullen (1969:14, 18). A healthy young lioness was killed by an adult lion during a territorial dispute (Bertram 1978:240).

Male lions dominate females at carcasses, thereby gaining differential access to the available meat. Lions eat slowly and with much snarling, swatting, and squabbling on larger carcasses, and they

take sole possession of smaller carcasses (Bertram 1979). Schaller (1972:132), however, described lions as bolting their food while snarling and slapping at their companions. Lions scavenge not only from other species, but also from each other (Bertram 1978:127). Males often appropriate small prey from the females. Schaller (1972:132-133) reported that 45 out of 60 gazelles that he saw male lions eating, and of which he knew the origin, were taken from lionesses.

Generally little or no competition is shown among male lions of the same coalition for a female in heat; the first male to find the female maintains possession as long as he stays close by her (Schaller 1972:132; Bertram 1979). Beneath this semblance of order, however, intra-coalition competition for females is widespread (Packer and Pusey 1982): The males sometimes race each other to the female, and they threaten or occasionally fight each other when possession of the female is unclear.

A lioness ate the cubs of another lioness which had intruded into her territory (Schaller 1972:220). At another time, two males intruded into another lion pride's area and killed a litter of three cubs, eating 1 or 2 of them (Schaller 1972:220). Schaller (1972:428) reported a total of 11 lion cubs killed by other lions. Four instances of adult male lions killing cubs were reported by Bertram (1978:99). Male lions taking over a pride sometimes kill the cubs they find there (Bertram 1975b; 1976). Craig Packer and Anne Pusey found that when new male lions entered a pride of females, the males killed the cubs in 17 of 19 cases (Caro 1984).

Lions compete with each other for meat, sometimes violently, but relations within a pride generally are peaceful (Bertram 1978:69).

When food is scarce for lions, the cubs are the first to do without (Bertram 1978:68-69; 1979). Females commonly take food from the cubs (Schaller 1972:133).

10.3.b Spotted Hyena

Spotted hyenas often have fights between adjacent clans, resulting from disputes over a carcass or a territorial boundary. These sometimes result in death (Kruuk 1972a:251-265; 1975b). In the Ngorongoro Crater, 36 of 109 prey kills resulted in disputes with a neighboring clan; four spotted hyenas were killed and three were badly injured (Kruuk 1972a:256). Fights also occur between individuals within a clan, usually over food and the protection of offspring (Kruuk 1972a:224-226). Young spotted hyenas are sometimes cannibalized by strangers (Kruuk 1972a:243, 246). Near the upper Seronera River, a hyena was seen carrying and eating a three-quarters grown dead spotted hyena (Cullen 1969:132). Of 22 spotted hyenas found dead, 14% were killed by other hyenas (Kruuk 1970).

Spotted hyenas compete for meat at a carcass by eating faster, and thereby consuming more, than their companions (Kruuk 1972a:268). They also carry away pieces of the carcass to eat alone (Kruuk 1975a:18).

10.3.c Cheetah

Aggression among adult male cheetahs is a common occurrence, with sometimes fatal results (G. and L. Frame 1981:185-188, 207, 213-216). Adult male cheetahs sometimes attack adult females and their large cubs (H. van Lawick 1977:30, 168-169; G. and L. Frame 1981:212).

Adult female cheetahs, in contrast, do not fight, but often seem

indifferent or actively avoid meeting each other (G. and L. Frame 1981:67, 103).

10.3.d Leopard

The leopard in the Serengeti ecosystem is relatively unstudied, and there are no published accounts of intraspecific competition.

10.3.e African Wild Dog

African wild dog packs are aggressive when they meet, and one pack usually chases the other away (G. and L. Frame 1981:107, 164, 200-204). Wild dogs often fight and sometimes kill to obtain a mate (L.H. Frame et al. 1979; G. and L. Frame 1981:48, 121, 192-195). But much more of the competition for reproductive opportunities is more subtle, and takes place within the pack rather than between packs (L.H. Frame and G.W. Frame 1976; L.H. Frame et al. 1979; G. and L. Frame 1981: 110-122, 151-154; L.H. Frame 1985b).

10.3.f Black-backed Jackal

Black-backed jackals fight over territorial boundaries, with the aggression occurring between individuals of the same sex (Moehlman 1979). When different pairs or family groups meet at the same carcass, they threaten and chase each other (Lamprecht 1978a).

10.3.g Common Jackal

Different pairs or family groups seldom met at the same carcass, although several times another pair watched from 200 to 300 m away without approaching (Lamprecht 1978a).

10.3.h Avian Scavengers

Most of the fights among vultures at carrion are between members of the same sex, and the aggressiveness of each species was described and quantified by Kruuk (1967).

10.4 Competition Foci

Interference competition clearly occurs among and within all the ungulate-eating species. The fact that so many examples have been recorded suggests that interference competition among the Serengeti's carnivores must be a common occurrence.

The many examples involving cleptoparasitism seem to be reasonable evidence that biologically meaningful losses of food resources do occur. The individual that loses in each interaction either has to make do with less food or try to replace it at a cost in energy, time, risk of injury, and risk of losing dependent offspring that are left unattended.

Many of the cases of fighting and direct killing of carnivores by carnivores are unequivocal in their meaning as important interference competition effects. In instances where the victims were eaten, it is perhaps a matter of definition whether they are examples of predation, interference competition, or both.

Not all the interactions among the Carnivora are costly. Some benefits obviously must occur to the winners of the competitive interactions, and in some cases both protagonists might cause positive gains for each other. Cheetahs and African wild dogs, because of their

contrasting hunting methods, might in an evolutionary sense benefit one another by preventing gazelles from evolving escape behavior and physical adaptations that are completely effective against either predator (Bertram 1979).

Within social species, when individuals cooperate to defend a territory or to catch large prey, they are in competition with conspecifics outside (and even inside) the group. This cooperation occurs among the Serengeti's lions (Schaller 1972:248-251, 259; Bygott et al. 1979; Packer and Pusey 1982), male cheetahs (G. and L. Frame 1981:207-216), spotted hyenas (Kruuk 1972a: 263-265), African wild dogs (Malcolm and H. van Lawick 1975), and jackals (Lamprecht 1978a; Moehlman 1979), but apparently does not occur among leopards. When several lions stalk prey together, they usually are twice as successful in catching it as is a single lion (Schaller 1972:357). Also, by hunting together, lions increase the range of the food sizes that they can use (Schaller 1972:357). Individuals striving to maximize their genetic fitness must overcome competition with individuals in their group, outside their group, and from other species.

If prey availability is an important factor determining niches of large predators, then the Serengeti carnivores should respond to the seasonal variations in food abundance that occur on the plains by shifting their use of the food resource and the ways in which they exploit that resource. The daily ungulate carcass density from non-predatory mortality on the Serengeti Plains in the wet season is about 1 per 33 sq km, while in the dry season it is probably less than 1 per 300 sq km (Houston 1979). A similar seasonal shift in availability of live prey on the Serengeti Plains was demonstrated by

the prey:predator ratios discussed in Section 6.3. The Serengeti Plains Carnivora experience a scarcity of food in the dry season, i.e. a decrease in the relative abundance of ungulates per predator and a decrease in the predictability of where these prey will be, with a resultant increase in interference competition. Food shortages are indicated by the observations of starvation among Carnivora of all ages, e.g. cheetahs (H. van Lawick, pers. comm., cited in G.W. Frame and L.H. Frame, in prep.) and lions (Schaller 1972:478).

In a review of the feeding behaviors of the Serengeti's five largest Carnivora, Bertram (1979) concluded that exploitation competition among these species probably is minute, because no one carnivore species appreciably reduces the supply of prey that is available to the others. However, within localities, prey sometimes become very scarce, and cleptoparasitism, disturbance of prey, and aggression among carnivores can essentially make food unavailable in these situations.

In Ngorongoro Crater, the seasonal prey:predator ratios reflect a more constant year-round environment than that of the Serengeti Plains. More food is available per predator in Ngorongoro Crater than on the dry-season Serengeti Plains. Although the dry-season prey:predator ratios are not very different between the Ngorongoro Crater and the Serengeti Plains (37:1 versus 28:1), the densities of perissodactyls and artiodactyls in the two places are substantially different. The prey density in the Ngorongoro Crater is about four times that on the Serengeti Plains in the dry season (102/sq km versus 24/sq km), but only about one-third of the Serengeti Plains' wet-season density of perissodactyls and artiodactyls (90 or 102/sq km versus 272/sq km).

Perhaps of greater significance is the unpredictability of prey distribution on the vast Serengeti Plains during the dry season; in some localities there are virtually no prey.

Nearly all the large Carnivora obtain large amounts of food by scavenging. The exception is the cheetah, which obtains less than 0.5% of its food this way (G.W. Frame and L.H. Frame, in prep.; see also Caro 1982). Lions on the Serengeti Plains scavenged substantially more of their food items than did those which lived in the woodlands (Schaller 1972:213). Lions obtain 10 to 15% of their diet by scavenging (Bertram 1979:223; Schaller 1972), leopards 5 to 10% (Bertram 1979:223), spotted hyenas 33% (Kruuk 1972a), and African wild dogs 3% (Schaller 1972). Some estimates indicate that all three jackal species depend very little upon ungulate meat from scavenging or hunting: Houston (1979) wrote, based on fecal analysis, that their diet is only 3% ungulate meat.

Other researchers have summarized the competitive relationships among the large Carnivora as follows: Lions do not experience any significant interference competition from the other Carnivora, in the opinion of Bertram (1979:223) who studied lions in the Serengeti woodlands and woodlands edge. Spotted hyenas scavenge considerable quantities by appropriating from all species, and they in turn lose much of their prey to lions, jackals, and vultures (Kruuk 1972a:148). The leopard's behavior of carrying its prey up into the safety of trees may be testimony to the significance of prey loss through interference competition. Between African wild dogs and spotted hyenas, cleptoparasitism occurs in both directions, probably mainly on the number of individuals involved and the extent of hunger

(Schaller 1972:338). In Kruuk's (1972a:141) view, African wild dogs generally dominated spotted hyenas, but the outcome of their interactions depended upon the number of individuals present, degree of hunger, previous experience, and individual differences. However, my conclusion is that spotted hyenas more often dominate the wild dogs (L.H. and G.W. Frame, unpubl. data). The spotted hyena is the most important robber of prey from both jackal species (Lamprecht 1978a). Both jackal species minimize these losses by dividing their prey, eating quickly, and caching rapidly (Lamprecht 1978a).

Within species of large Carnivora, the most intense competition observed generally was in territorial defense, a prerequisite for obtaining vital resources and reproductive opportunities.

Causes other than predation make many carcasses available to all scavengers. Houston's (1980) study of the interrelations of scavengers in the Serengeti indicated that 11 species of birds and five species of mammals often fed from the carcasses of ungulates which had died from causes other than predation. The present study concentrated on predator-killed prey, with the result that the kite, white-naped raven, and bateleur were never recorded as feeding on carcasses. Among these, however, white-naped ravens on several occasions searched around African wild dog dens containing pups, apparently finding tiny pieces of regurgitated meat and perhaps pup feces (L.H. and G.W. Frame, unpubl. data). There is one reported instance of vultures eating alive an old disabled topi, which was unable to defend herself (Cullen 1969:48). Kruuk (1967) thought that the lappet-faced and white-headed vultures sometimes caught gazelle fawns. Four vultures (African white-backed, Rüppell's, white-headed, and lappet-faced) and the

marabou stork collectively eat 98% of the meat consumed by scavenging birds in the Serengeti (Houston 1978). White-backed vultures, Rüppell's vultures, and lappet-faced vultures are not only the three most abundant vultures, but their feeding habits make them the three species most likely to interfere with the large mammalian carnivores (Kruuk 1967). Vultures generally seem to benefit more from their association with mammalian carnivores than the reverse (Kruuk 1967).

This chapter concludes with my subjective assessment of the relative intensities of the competitive relationships among the seven ungulate-eating Carnivora species. The interactions are rated according to the apparent frequency and overall seriousness of the interference competition to genetic fitness. The dominant member of each dyadic interaction is identified in the matrix of all pairwise interactions (Table 10.1). Insufficient information prevents an evaluation of the carnivorous birds by species. The four foci of most intense competition, based on the above review of the Serengeti competition literature, are: (1) lions and spotted hyenas involved in a two-way struggle, (2) spotted hyenas dominating both jackal species and the scavenging birds, (3) spotted hyenas dominating African wild dogs, and (4) cheetahs being dominated by lions, spotted hyenas, and vultures. The spotted hyena versus African wild dog interaction is probably the most important for wildlife management concerns, because it appears to be responsible for a decline in African wild dog numbers (Frame et al. 1979), as discussed in Chapter Nine.

Table 10.1 Subjective assessment of the relative intensities of interference competition between all species pairs of the ungulate-eating Carnivora on the Serengeti Plains. Intensity of competition, expressed as impact of superior on inferior competitor: s = slight, m = moderate, e = extreme. Species are listed in order of decreasing body weight. Some dyads are listed twice because interference (aggression, killing, cleptoparasitism) occurs in both directions.

	Superior Competitor							
	Lion	Spotted Hyena	Cheetah	Leopard	African Wild Dog	Black-backed Jackal	Common Jackal	Carnivorous Birds
Inferior Competitor								
Lion		m		s				s
Spotted hyena	m				s	s	s	s
Cheetah	m	m		s				m
Leopard	s	s						
African wild dog	s	e						
Black-backed jackal	s	m	s	s	s			s
Common jackal	s	m	s	s	s			s
Carnivorous birds	s	m			s	s	s	

CHAPTER XI

CHEETAH SEX-, AGE-, AND SOCIAL-GROUP YEAR-ROUND NICHES

11.1 Similarity Suggests Competition

As species-niche constructs are useful for considering the interactions among species, the niche constructs of sex, age, and social groups are useful for examining within-species interactions. Similar patterns of the niche dynamics that occur among species should also occur within species. The most-similar group types are most likely to compete for resources.

My working hypothesis is that the sex, age, and social groups of cheetahs in the Serengeti ecosystem are different in their uses of habitat, prey, time, and other resources. Cheetahs occur in five group types as follows:

Adult female alone or with cubs up to 10 months old,

Adult female with cubs older than 10 months,

Sub-adult littermate group that has separated from its mother,

Solitary adult male, and

Adult males in a group.

These represent all possible solitary and group occurrences among cheetahs, except for consortships. Consort groups are not considered because they do not hunt. I predict that adult male groups differ most from the others, because male territorial behavior restricts their movements, and living in coalitions influences them to hunt larger prey (G.W. Frame and L.H. Frame, in prep.).

I collected field data on what appeared to be biologically meaningful niche measures for the purpose of describing cheetah behavior and ecology in a detailed and quantitative manner. Data on resource use and activity times of cheetahs were collected in the manner described in Sections 3.1 and 3.2.a. For the present analyses I consider only my data associated with hunting activities. These data are tallied and compared for categories of sex, age, and association. Each group type is a composite of at least several different individuals, or of several groups of that particular type.

11.2 Cheetahs in Five Group Types

Intraspecific niches for five cheetah group types are described from the variables that were measured during cheetah hunts, where a hunt is defined as one or more of the following food-getting activities: Traveling to find prey, approaching, stalking, rushing, chasing, capturing, and eating. Further details of the components of cheetah hunts are discussed in G.W. Frame and L.H. Frame (in prep.). Activities associated with feeding are likely to provide the greatest separation of group niches.

The data were recorded during 495 successful and unsuccessful hunts. They represent 80 occupied resource states on nine niche axes. The total number of observations is 3,047. The axes are: Prey body weight hunted, habitat density, time of hunting, prey species hunted, prey density, weather, prey group size, hunting technique, and length of chase (Appendix G). Because of the searching method that I used during field work, the relative proportion of cheetah group types that I recorded hunting probably closely approximates their actual

occurrence (cf. Section 3.1).

From the cluster analysis of the five cheetah group types, the adult male coalitions differ most from the other group types (Fig. 11.1). This analysis is performed using the marginal totals only (cf. Section 3.2.b). The resemblance matrix and cophenetic correlation are given in Table I.14 (Appendix I).

Non-circular niche metrics show that adult male cheetahs living in groups are most generalized in their hunting ecology and behavior, as indicated by the widest niche breadth (Table 11.1). The most similar group types, as indicated by the largest niche overlap, are: (1) adult females alone or with cubs less than 10 months old, and (2) adult females with cubs older than 10 months (Table 11.2). The most different group types are solitary adult males and adult males living in groups. Mathematical results for each axis, calculated in three ways, are in Table V.1 in Appendix V.

Comparisons are made of the three out of nine niche axes where statistically significant differences exist among the cheetah group types in their use of resource states. The results for each axis are:

Axis I comprises the body weights of prey individuals that were hunted. The differences in the frequency of occurrence of two prey-weight categories utilized by the five cheetah group types are statistically significant ($X^2 = 97.81$, df = 4, $p < 0.001$, two-tailed). The percent frequencies are shown in Figure 11.2.

Axis II comprises the habitat densities or physiognomic vegetation types where cheetahs were seen hunting. The test result shows no statistically significant difference in the occurrence of the five cheetah group types among two cover types ($X^2 = 11.53$, df = 4, $p < 0.05$,

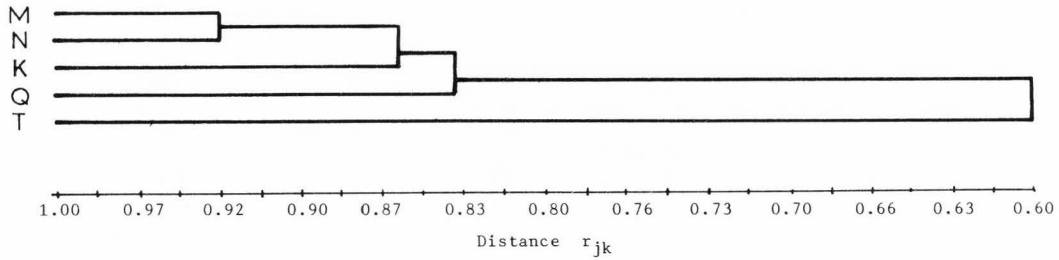


Figure 11.1 Dendrogram of five cheetah group types, showing similarity in behavior and resource use during hunts. The hunts are measured by 80 resource states on nine axes (using marginal totals) in the Serengeti ecosystem. Abbreviations: M = adult female alone or with cubs $\leq$ 10 mo. old, N = adult female with cubs > 10 mo. old, K = sub-adult littermates after leaving their mother, Q = adult male alone, T = adult males in a group. Data are from Appendix G.

Table 11.1 Niche-breadth relationships year-round among five kinds of cheetah groups. The species are listed in order of decreasing non-circular niche breadth. The three methods of calculation are used on the data in Appendix G; the mathematical results are in Table Y.1 of Appendix Y. Abbreviations: M = adult female alone or with cubs $\leq$ 10 mo. old, N = adult female with cubs > 10 mo. old, K = sub-adult littermates after leaving mother, Q = adult male alone, T = adult males in a group.

Relative Niche Breadth	Product Method	Summation Method	Projection Method
Widest breadth	T	T	T
	N	N	N
	M	M	K
	K	K	M
Narrowest breadth	Q	Q	Q

Table 11.2 Niche-overlap relationships year-round among five kinds of cheetah groups. The species-pairs are listed in order of decreasing non-circular niche overlap. The three methods of calculation are used on the data in Appendix G; the mathematical results are in Table Y.2 of Appendix Y. Abbreviations: M = adult female alone or with cubs $\leq$ 10 mo. old, N = adult female with cubs > 10 mo old, K = sub-adult littermates after leaving mother, Q = adult male alone, T = adult males in a group.

Relative Niche Overlap	Product Method	Summation Method	Projection Method
Greatest overlap	MN	MN	MN
	MK	MK	MK
	MQ	MQ	MQ
	NQ	NQ	NK
	KQ	KQ	KQ
	MT	NK	NQ
	NK	MT	NT
	NT	NT	MT
	KT	KT	KT
Least overlap	QT	QT	QT

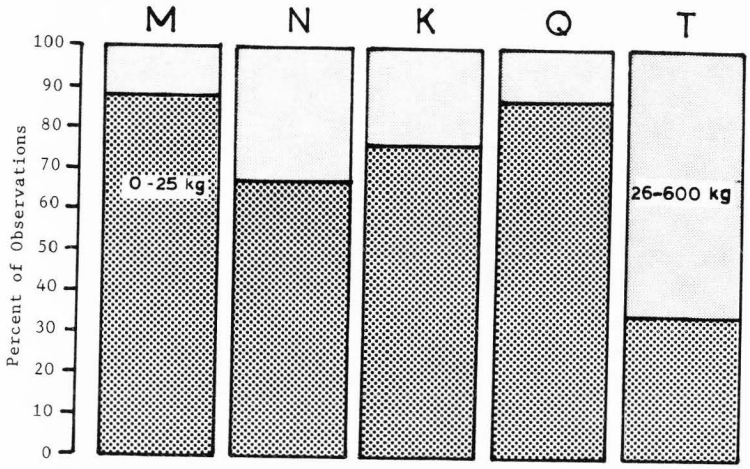


Figure 11.2 Percent frequencies in which cheetah group types hunted prey of various body weights. Abbreviations: M = adult female alone or with cubs $\leq$ 10 mo. old, N = adult female with cubs > 10 mo. old, K = sub-adult littermates after leaving their mother, Q = adult male alone, T = adult males in a group. Data are from Appendix G.

two-tailed). The p-level is not acceptable ($p = 0.01$ was specified in Section 3.2.d).

Axis III comprises the time of the day in which the most active part of each hunt occurred. The differences in the frequency of occurrence of hunts in two times of day by the five cheetah group types are statistically significant ($X^2 = 17.61$, $df = 4$, $p < 0.01$, two-tailed). The percent frequencies are shown in Figure 11.3.

Axis IV comprises the prey species that were hunted. The differences in the frequency of occurrence of the two prey types utilized by the five cheetah group-types are statistically significant ($X^2 = 68.87$, $df = 4$, $p < 0.001$, two-tailed). The percent frequencies are shown in Figure 11.4.

Axes V through IX comprise prey density, weather, prey group-size hunted, occurrence of stalking, and chase length in each cheetah sighting. On each of these axes the test criteria of minimum expected cell frequencies are not met.

The three statistically significant axes provide the basis for constructing a three-dimensional graph (Figure 11.5). These axes are the prey body weight (kilograms), diel time when the hunts occurred, and prey species hunted. The niche centers were plotted from the mode of the data (Appendix G) for each group type. The graph shows that males living in groups differ greatly from the other cheetah group types in hunting behavior and ecology.

The same three axes are considered for plotting the median for each cheetah group type as another way of describing their niche centers. The prey-species axis, however, is deleted because the species cannot be ordered, thereby precluding a median. The two-dimensional graph

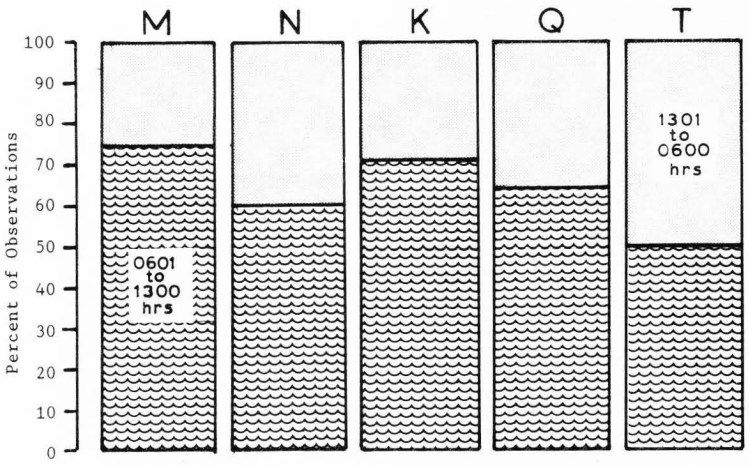


Figure 11.3 Percent frequencies in which cheetah group types hunted at various times of the day. Abbreviations: M = adult female alone or with cubs $\leq$ 10 mo. old, N = adult female with cubs > 10 mo. old, K = sub-adult littermates after leaving their mother, Q = adult male alone, T = adult males in a group. Data are from Appendix G.

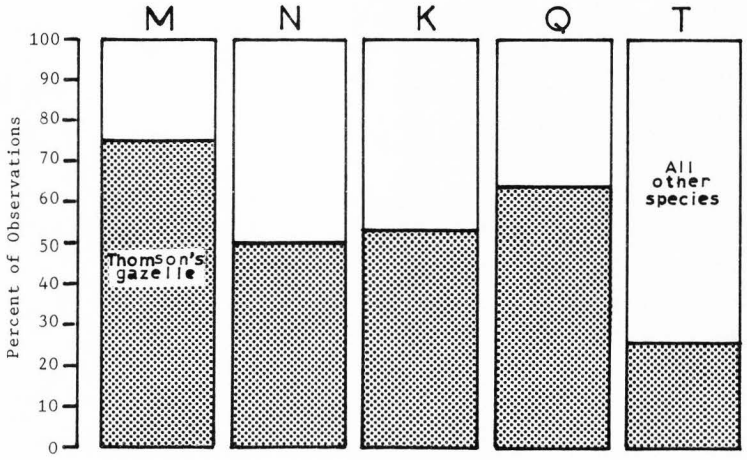


Figure 11.4 Percent frequencies in which cheetah group types hunted for various prey species. Abbreviations: M = adult female alone or with cubs $\leq$ 10 mo. old, N = adult female with cubs > 10 mo. old, K = sub-adult littermates after leaving their mother, Q = adult male alone, T = adult males in a group. Data are from Appendix G.

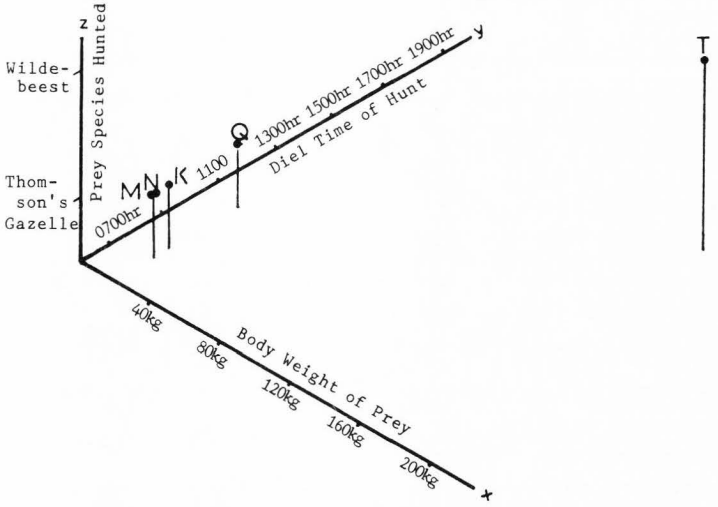


Figure 11.5 Niche centers of five cheetah group types, as defined by the mode of each group on three axes during hunting. Data are from Appendix G. Abbreviations: M = adult female alone or with cubs $\leq$ 10 mo. old, N = adult female with cubs > 10 mo. old, K = sub-adult littermates after leaving their mother, Q = adult male alone, T = adult males in a group.

(Fig. 11.6) again suggests that males living in groups differ markedly from the other cheetah group types.

11.3 Discussion

Adult male cheetah coalitions show the greatest breadth in resource use among all five group types, while solitary males show the narrowest. Two explanations are apparent: The time spent patroling the territory to mark and investigate marks, and to search for intruders and potential mates, must make the niche of territorial males different from adult females, cubs, and littermates who are not territorial. Second, adult males are larger than females, and the combined strength of several males in a cooperative hunting group enables them to capture larger prey more regularly than the other group types. Males, living in a group for reasons other than hunting, also need to catch larger prey to feed the entire group, so the group can stay together. Otherwise, the group would have to spend substantially more of its time hunting, or jeopardize its alliance by hunting separately. The self-benefit for males living in a coalition must be increased opportunities for fathering offspring during their lifetime (G.W. Frame and L.H. Frame, in prep.). The extremely narrow niche breadth of solitary males probably is due partly to the very small sample size for this category, but it is also reasonable to expect an individual cheetah to be less variable than the combined variability of several individuals that are living together.

The highest niche overlaps were between adult females (alone or with cubs up to 10 mo. old) and all other groups, except the adult male coalitions. Four explanations are apparent (cf. G.W. Frame and L.H.

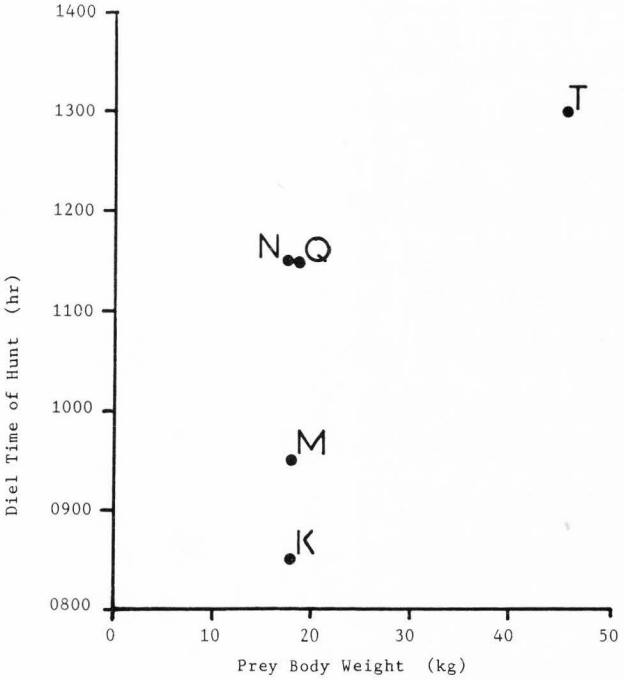


Figure 11.6 Niche centers of five cheetah group types, as defined by the median of each group on two axes during hunting. Data are from Appendix G. Abbreviations: M = adult female alone or with cubs $\leq$ 10 mo. old, N = adult female with cubs > 10 mo. old, K = sub-adult littermates after leaving their mother, Q = adult male alone, T = adult males in a group.

Frame, in prep.): First, mothers with dependent cubs must hunt more often than male coalitions do. Second, small cubs are prone to divert their group's hunting to whatever attracts their attention even if it is not a cheetah's usual prey. Third, adult females are more mobile than are territorial males, except for the six weeks when tiny cubs are confined to lairs. Fourth, mothers with cubs in a lair must spend more of their time in areas of dense vegetation to minimize cub mortality.

Another level, which is not dealt with here, is that of the individuals within each of the cheetah group types. Individuals strive to maximize their own reproductive success above all, and secondarily their kin's (Maynard Smith 1964; Trivers 1985:20). Individual niches (sensu MacMahon et al. 1981) will be described elsewhere for the Serengeti's cheetahs (G.W. Frame and L.H. Frame, in prep.) and African wild dogs (L.H. and G.W. Frame, unpubl. data). For the Serengeti's other Carnivora, individual niche and social-group niche differences are readily apparent from reading the behavioral descriptions (cf. Appendix C).

Male cheetahs that form coalitions for territorial defense potentially are superior competitors on more than one resource axis ("super" in the sense of Tilman 1982:247). They tend to hunt a larger range of prey sizes, and they are better able to sequester preferred habitat. The presumed biological benefit is increased breeding opportunities.

In conclusion, the variations in how and when cheetahs use the available resources are at least partly a consequence of the different resource requirements resulting from their social roles. Their niches do not suggest any efforts by the cheetahs to reduce intraspecific

exploitation competition for food and habitat. Intraspecific niches are discussed further in Chapter Fourteen.

CHAPTER XII

FORCES SHAPING THE CARNIVORE COMUNITY

12.1 Are There Predictable Community Patterns?

This chapter examines four hypotheses about the structure of competitive communities. The data are those of the large and medium-sized Carnivora in the Serengeti ecosystem. The applicability of these hypotheses is discussed with regard to the background conditions and the kinds of data that are required. If these hypotheses are to be testable, they must be assumed to describe proximate behavioral adjustments by the organisms, rather than the evolutionary results of selection forces.

12.2 The Niche-breadth-variation Hypothesis

Niche breadth is predicted to be larger in uncertain environments than in environments with greater environmental certainty (MacArthur and Levins 1967:385; Levins 1968:45; MacArthur 1972; Leigh 1975). This might be seen as differences between localities where the predictability of the resources varies. The greater buffering and certainty of a stable environment should lead to a greater degree of specialization, i.e. a narrower niche breadth, than occurs in a varying environment. Larger niches in variable environments have been shown for reptiles and amphibians (Inger and Colwell 1977: 242-243), migratory shorebirds (Baker and Miller Baker 1973), and rodents (Alcoze and Zimmerman 1973).

Consistent with this hypothesis, large and medium-sized Carnivora should have broader niches on the Serengeti Plains, where the prey are migratory (a variable and unpredictable environment with regard to food) compared with the nearby Ngorongoro Crater, where prey are predominantly non-migratory (an unvarying and predictable environment with regard to food). This was the rationale for the analyses in Chapter Eight. Prey species are nearly identical in both localities (cf. Tables 2.4 and 2.6).

The prediction is tested here by the null hypothesis of no differences in niche breadths of large and medium-sized Carnivora species on the Serengeti Plains and adjacent woodlands compared with the Ngorongoro Crater. The alternative hypothesis is that niche breadths are larger on the unpredictable Serengeti Plains. A major assumption is that food types utilized are an adequate measure of carnivore niches. The null hypothesis will be rejected if $p \leq 0.01$.

Non-circular niche breadths are computed from food types hunted or eaten by seven large and medium-sized Carnivora in the two locations (Tables 8.1 and 8.2). The randomization test (B.F. Green 1977) is used on the paired data. For each Carnivora species the niche-breadth value in one location is entered as the "before" condition and the value in the other location is entered as the "after" condition. Each niche-breadth value is entered as the number of percentage points out of a possible 100, rather than as a decimal proportion of 1.00.

Of the seven niche breadths, six measured larger in the variable environment of the Serengeti Plains (Tables 8.1 and 8.2). Application of the randomization test to these data shows that niche breadths are larger on the Serengeti Plains, with a one-tailed value of $p = 0.023$.

The null hypothesis of no difference cannot be rejected.

Therefore, the Serengeti ecosystem large and medium-sized Carnivora data do not confirm the hypothesis of larger niche breadths in more-variable environments. The apparent difference is not different statistically.

The above test used niche breadth values that were calculated from different weighting factors for the two locations (cf. Section 3.2.c). Another test of the null hypothesis is to combine both data sets and consider simultaneously, with the same eco-assay niche weighting factors, all the food-habits data. The logic of this approach is that the seven Carnivora from the Serengeti Plains and the Ngorongoro Crater are all part of the same populations in the same ecosystem, even though the environment differs locally. Their food-habits data are in Appendices W and X. In this approach each Carnivora species has a separate niche breadth calculated from each location's data set, as if the carnivore is two different species in one location. For example, lions on the Serengeti Plains are treated as a different species from lions in the Ngorongoro Crater. Thereby, the same niche weighting factors are used for both locations in the ecosystem. The randomization test is used on paired data, and the data are again entered as percentage points rather than as decimals.

The combined data from the two locations (Table 12.1) show that non-circular niche breadths measured larger for six of the seven Carnivora in the variable environment of the Serengeti Plains, with a one-tailed value of $p = 0.031$. The null hypothesis of no difference cannot be rejected. Therefore, the Serengeti ecosystem ungulate-eating Carnivora data again do not support the hypothesis of larger niche

breadths in a more-variable environment. As was true in the preceding test, the apparent difference is not different statistically.

Table 12.1 Niche breadths of seven large- and medium-sized Carnivora in a variable environment compared with a stable environment.

Carnivora Species	Niche Breadths	
	Variable Environment (Serengeti Plains)	Stable Environment (Ngorongoro Crater)
Lion	.42	.35
Spotted hyena	.37	.26
Cheetah	.17	.15
Leopard	.28	.03
African wild dog	.33	.29
Black-backed jackal	.55	.41
Common jackal	.43	.47

Although the niche-breadth-variation hypothesis is not supported by these tests using Carnivora food-habits data, the results are rather suggestive. If the reader accepts a slightly less rigorous p-value, the null hypothesis can be rejected, and the alternative hypothesis of larger niche breadths on the unpredictable Serengeti Plains can then be accepted. Also, a data set collected in a more consistent manner for all seven Carnivora in both locations might give statistically significant results.

In summary, the niche-breadth-variation hypothesis cannot be

confirmed by either of the two tests of Carnivora niche breadths at a stringent probability level. Thus, the Serengeti ecosystem's large and medium-sized Carnivora do not support the hypothesis of broader food niches in a variable environment. However, niche breadths may not be adequately measured by food types eaten, and other niche axes perhaps should be considered.

12.3 The Niche-overlap-variation Hypothesis

Niche overlaps are addressed here, using the same data that provided the niche-breadth measurements in the preceding section. Niche overlap between coexisting species pairs is predicted to be larger in more-stable environments than in variable ones (Levins 1966; MacArthur and Levins 1967; MacArthur 1972; May 1973, 1974). A study of fishes provided support for this hypothesis (Zaret and Rand 1971). However, a study of reptiles and amphibians in Asia found similar niche overlaps in both kinds of environments (Inger and Colwell 1977:242, 244) and failed to confirm the hypothesis.

Consistent with this hypothesis, large and medium-sized Carnivora should have smaller niche overlaps in the variable prey environment of the Serengeti Plains compared with the relatively stable prey environment of the Ngorongoro Crater. The latter location essentially is stable for carnivores, because a permanent supply of water and forage allows most of the ungulates to remain there throughout all seasons.

The prediction of less niche overlap in a variable environment will be tested by the null hypothesis of no difference in pairwise niche overlaps among the large carnivore species on the Serengeti Plains and

adjacent woodlands compared with the Ngorongoro Crater. The alternative hypothesis is that niche overlaps are larger at the stable Ngorongoro Crater location. A major assumption is that food alone is an adequate measure of carnivore niches. The null hypothesis is rejected if $p \leq 0.01$.

Non-circular niche overlaps are computed from data of food types eaten (Tables 8.1 and 8.2). The randomization test is used on the paired data. For each Carnivora species, the niche-breadth value in one location is entered as the "before' condition and the value in the other location is entered as the "after" condition. Niche overlap values are entered as the number of percentage points out of the possible 100, rather than as a decimal proportion of 1.00.

Of the 21 species-pair niche overlaps, 17 measured smaller at the Ngorongoro Crater (Tables 8.1 and 8.2). Application of the randomization test to these data shows that niche overlaps are smaller at Ngorongoro Crater, with a one-tailed value of $p < 0.001$. The null hypothesis of no difference is, therefore, rejected. The direction of the difference is, however, opposite to that which was predicted. Therefore, the Serengeti ecosystem's large and medium-sized Carnivora data do not confirm the hypothesis of larger niche overlaps in more-stable environments.

Another test of the null hypothesis is to consider simultaneously all the food-habits data, as is done in the second method of Section 12.2, so that the same niche-weighting factors are used for both locations. The data are of the seven Carnivora from the Serengeti Plains (Appendix W) and the Ngorongoro Crater (Appendix X), for which are calculated separate niche overlaps for each species in each

location. For example, the overlap of lions and spotted hyenas on the Serengeti Plains is treated as a different species-pair overlap from that of lions and spotted hyenas in the Ngorongoro Crater, but species-pair overlaps between the two locations are deleted. Thus, the same niche-weighting factors (cf. Section 3.2.c) are used for both locations, unlike the analyses in Chapter Eight. The randomization test again is used, with the data entered as percentage points rather than as decimals.

The combined data from the two locations (Table 12.2) show that non-circular pairwise niche overlaps among the seven Carnivora again measured smaller in 17 of the 21 species in the more-stable environment of the Ngorongoro Crater. Application of the randomization test to the data in Table 12.2 shows that niche overlaps are smaller at the Ngorongoro Crater, with a one-tailed value of $p < 0.001$. The null hypothesis of no difference is, therefore, rejected. The direction of the difference is, however, opposite to that which was predicted. Therefore, the Serengeti ecosystem large and medium-sized Carnivora data do not support the hypothesis of larger niche overlaps in more-stable environments.

The niche-overlap-variation hypothesis clearly is not supported by these tests using Carnivora food-habits data. Either the hypothesis is incorrect, or else the data are inadequate. The smaller niche overlaps in the Ngorongoro Crater might be due to the smaller sample sizes in that location. Further testing can adjust for the difference in sample sizes between the Serengeti Plains and adjacent woodlands and the Ngorongoro Crater locations. Food records can be randomly selected from the data of each carnivore species in the Serengeti location,

until the sample sizes are the same as those at Ngorongoro. Recomputing the niche overlaps would provide more comparable data, to which the randomization test can be applied.

In summary, the niche-overlap-variation hypothesis was rejected by the two tests of carnivore niche overlaps. The Carnivora had less overlap in their food niches in the stable environment of Ngorongoro Crater.

Table 12.2 Niche overlaps of seven large- and medium-sized Carnivora in a variable environment compared with a stable environment. Abbreviations: H = spotted hyena, C = cheetah, P = leopard, D = African wild dog, B = black-backed jackal, J = common jackal.

Carnivora Species	Niche Overlaps											
	Variable Environment (Serengeit Plains)						Stable Environment (Ngorongoro Crater)					
	H	C	P	D	B	J	H	C	P	D	B	J
Lion	.99	.74	.80	.94	.91	.84	.95	.40	.01	.81	.94	.85
Spotted hyena		.74	.81	.95	.90	.84		.14	.02	.67	.89	.76
Cheetah			.98	.86	.67	.86			.00	.77	.52	.63
Leopard				.91	.73	.91				.04	.00	.01
African wild dog					.85	.89					.85	.85
Black-backed jackal						.90						.95

12.4 The Range-of-food-items Hypothesis

According to Schoener (1971:381), the lower the amount of food that is available, the greater the range of food types that should be selected. The alternative prediction that organisms specialize when food is limited was suggested by Landres and MacMahon (1980). Interspecific subordinates should more readily modify their behavior as conditions change, because they have less choice of the resources (Morse 1974:823-824).

The range of food items selected by cheetahs during 212 successful hunts and by African wild dogs during 455 successful hunts on the Serengeti Plains are compared by season. The data (Appendix O) are from the unpublished observations of G.W. Frame and L. Herbison Frame. This is an extension of the seasonal food-habits analyses of Chapter Seven, where wet season is defined as November through May and dry season is June through October.

The prediction is that more kinds of foods are selected when food is in short supply. The two null hypotheses are that there is no difference in the food items successfully hunted by cheetahs (or African wild dogs) on the Serengeti Plains in the wet season compared with the dry season. The alternative hypothesis is that the diet is more varied in the dry season. The null hypothesis is rejected if $p \leq 0.01$.

The randomization test is used for paired data. One test uses the paired wet-season and dry-season observations of cheetahs, and a second test uses the same kind of African wild dog data. The tests are

performed by entering the number of observations that each prey type was utilized in one season as the "before" condition, and the number of observations in the other season as the "after" condition. Only the 12 food types eaten by cheetahs and the 16 eaten by African wild dogs at some time of the year are used as the number of pairs in each randomization test. In both seasons other prey species are available (cf. Table 2.4), but they are not successfully hunted. During much of the dry season, when there is less food on the Serengeti Plains, the migratory wildebeest, zebras, and topi generally are unavailable.

Results are consistent for the two predators. The cheetah's range of prey types decreased from 11 species in the wet season to eight in the dry season. The randomization test shows a one-tailed value of $p = 0.089$, so the null hypothesis of no differences in not rejected. The African wild dog's range of prey types decreased from 12 in the wet season to 10 in the dry season. The randomization test showed a one-tailed value of $p = 0.286$, so the null hypothesis of no differences again is not rejected. Neither the cheetahs nor the African wild dogs provide evidence to support the range-of-food items hypothesis that more kinds of foods are eaten when food is scarce.

A simple count of the number of prey types recorded at least once in the diet in each season also would have failed to reject the null hypothesis. If we assume that all prey species were available in both seasons, cheetahs and African wild dogs both show a narrower range of food types successfully hunted at the time of year when the lower amount of food is available. Even allowing for the two or three migratory prey species that were absent from the Serengeti Plains during much of the dry season, the cheetahs and African wild dogs show

no change in number of prey types successfully hunted in the two seasons. So, again, there is no support for the hypothesis that a wider range of food types is selected when food is scarce.

Failure of prey availability to coincide exactly with the two seasons confounds the problem. There is lag time, and there is unpredictability. This is the reason why the hypothesis was tested with the number of observations of each prey species by season, rather than merely whether or not the prey species was recorded at least once.

The hypothesis can be better tested by defining the wet season and dry season by prey density rather than by calendar dates. But that requires an arbitrary decision of what density constitutes a "low" amount of prey.

In summary, the range-of-food-items hypothesis cannot be confirmed by either of the tests. Cheetahs and African wild dogs on the Serengeti Plains appear not to select a different diet when food is in short supply, or, if they do, their diet appears to be more varied when food is abundant.

12.5 The Niche-inclusion Hypothesis

The niche-inclusion model states that when interference mechanisms are involved in the competitive interaction between a generalist and a specialist, the specialist should successfully outcompete the generalist (Colwell and Fuentes 1975:291-292; Morse 1974). Because the outcome is known *a priori*, a null hypothesis cannot be set up for rejection, although it is possible to assemble the evidence to show how the Serengeti's large and medium-sized Carnivora relate to this model.

If being a generalist is defined in terms of food habits, then cheetahs are the specialists among ungulate-eaters. The cheetahs have the narrowest food-niche breadth (cf. Tables 4.2 and 4.3). All the ungulate-eaters are successful in appropriating food from the specialist cheetah (cf. Section 10.2). The cheetah, however, does not even try to defend its food against intruding lions, spotted hyenas, leopards, or African wild dogs (G.W. Frame and L.H. Frame, in prep.). At the very least this increases the cheetah's costs in obtaining needed resources, thereby lowering its genetic fitness. By definition (cf. Section 1.3) this constitutes competition.

As a result, the niche-inclusion prediction seems to be opposite to what is occurring among the medium and large-sized Carnivora of the Serengeti Plains. When times are tough in the Serengeti, the generalist is more likely to succeed (cf. Chapter Nine).

In summary, the niche-inclusion hypothesis is not supported by comparing the specialist cheetah with its competitors. Among the Serengeti's ungulate-eaters, larger body size or hunting-group size confers the ability to interfere successfully with a specialist.

12.6 Discussion

Although food is a force shaping the Serengeti's carnivore community, the manner in which it exerts its influence is not clearly described by prevailing theory. None of the four hypotheses examined is supported by the food-habits data of the large and medium-sized Carnivora. Part of the problem must lie in defining what qualifies as a "varying" or a "stable" environment, when a situation is "uncertain" or "unpredictable," and how much food is a "low" amount.

The tests are ambiguous because the data for all the species considered were not collected in an entirely consistent manner. Another consideration is how much of the niche must be measured in order to test these hypotheses. Foods are used here because they probably are the most important single axis. But perhaps multidimensional niche metrics must be used to appropriately test these hypotheses.

The problem with the models is that their authors stated them simply and concisely. In biological systems, however, that leads to ambiguities. The hypotheses would lend themselves more readily to testing if they are accompanied by a set of specific conditions (cf. Colwell 1974). Or, as I have tried to do here, the particular background conditions in which the test is done, are specified.

The niche-breadth-variation hypothesis and the niche-overlap-variation hypothesis are not independent of each other. In an unpredictable environment such as the Serengeti Plains, the increase in niche breadths among the coexisting Carnivora must necessarily eventually result in increased niche overlaps on the same resource axis. The hypotheses as they are stated, however, seem to assume a wider assortment of resource states, so that in an unpredictable environment niches can broaden and overlaps can decrease at the same time. Use of multidimensional niche metrics in these tests might allow the Carnivora to reduce their overlaps along other axes where the use of resource states can be more flexible.

Another consideration is whether or not these hypotheses pertain to

species or to something more basic, such as individuals and hunting groups. In an ecological community the competition over food, for example, might be more intense among individuals of the same species than it is among individuals of different species.

The important point is that in this natural system the community models cannot be tested in any convincing way. A start in resolving this dilemma, from the field biologist's perspective, is to specify the assumptions and background conditions as they exist in the real world situation, and to test the hypothesis in that context. This approach will suggest ways in which the community models can be restated in more precise terms, so that ultimately the models might more accurately describe natural communities.

The Serengeti ecosystem data show community patterns that, except for niche breadths, are opposite of what current theory predicts. We saw in this chapter that the Serengeti carnivores have larger food-niche breadths and overlaps in varying and unpredictable environments. The range of a carnivore's food types is greater when food is abundant. And, in interference competition, the generalist successfully outcompetes the specialist.

CHAPTER XIII

ANALYSIS OF BODY SIZE

13.1 An Evolutionary Response to Competition

Predictable size differences in morphological features were discovered empirically from the results of numerous studies of mammals, birds, and invertebrates living in sympatry and allopatry (W.L. Brown and E.O. Wilson 1956). These size variations are measurable as differences in total body weight or as differences in the length of body parts, especially the feeding appendages. The size differences are inferred to be an evolutionary divergence under the pressure of competition.

The purpose of this chapter, therefore, is to examine the body weights and lengths of the Serengeti ecosystem's ungulate-eating mammals and birds. The carnivores of the Serengeti have coevolved in a competitive community for a very long time, so character displacement (sensu W.L. Brown and E.O. Wilson 1956) is expected. My working hypothesis is that the ungulate-eaters' body weights, and lengths of body parts, are displaced in a predictable pattern. This chapter differs from all of the preceding ones, in that it addresses evolutionary responses to competition rather than proximate responses.

Body weights of a number of species, ordered from smallest to largest on a one-dimensional food-resource continuum, were reported to form a geometric sequence--with each species about twice as massive as the next (May 1974:312; Horn and May 1977). For example, this ratio

was reported among species of African rain-forest squirrels occupying a given foraging level and habitat (Emmons 1980), coexisting desert rodents (R.S. Miller 1964:259; J.H. Brown 1975), and four feeding guilds of West Indian birds (Case, Faaborg, and Sidell 1983).

Similarly, the linear dimensions of skulls or beaks of cogeneric mammals and birds, when arranged in order of increasing body size, often seem to occur in a geometric sequence of 1.28 (range 1.2 to 1.4) among sympatric species and less when they are apart (Hutchinson 1959; Schoener 1965, 1974b). Ratios approximating these values are reported to occur within many different taxonomic categories. For example, species of African rain-forest squirrels occupying a given foraging level and habitat differ in body length by approximately 1.3 (Emmons 1980). Bird bill-length ratios vary from 1.00 to 1.87 (Schoener 1965). Among salamander species, body-length ratios are 1.35 to 1.40 (Hairston 1980) and 1.2 to 1.3 (Krzysik 1979). Coexisting spiders have body-length ratios of 1.02 to 1.34 (Uetz 1977). Mud snail species living together show differences in body-length ratios averaging 1.53 (range 1.23 to 1.95), but those living apart are the same size (Fenchel 1975). Fenchel's study of mud snails and Huey and Pianka's (1974) study of skinks are often cited as providing the most convincing evidence of morphological character displacement.

Eight obvious explanations for the existence of morphological character differences among coexisting species are: competition, predation, dispersal, hybridization, differential reproductive success, clines, reproductive isolation, and randomness.

The first and most commonly invoked explanation is competition (Pianka 1978:194). Among sympatric species, large ratios suggest the

existence of interspecific competition and small ratios are expected to be eliminated by competitive exclusion (Strong 1980). Size differences among consuming species are cited as examples of competitive release (Schoener 1968:724; Cody 1974:132-136). Larger-sized species generally can use a wider range of resources than can smaller species (D.S. Wilson 1975; Burger and Trout 1979), although certain limited resources might favor smaller body size (Wassersug et al. 1979). Competition-induced size differences also might occur between sexes of the same species. This was suggested by a study of Anolis lizards, the species of which have the greatest amount of sexual dimorphism in body size where there is minimal potential for interspecific competition, and the least amount of sexual dimorphism in body size when there is substantial potential for interspecific competition (Schoener 1968:724). Many examples of interspecific variations in body sizes occur among island species (e.g. Selander 1966; Schoener 1967; Rand 1967), although the differences occur in other settings too. There are, however, problems in dealing with ratio data when the size of individuals is dependent on both age and genotype (Lister and McMurtrie 1976).

Most competition is thought to be over limited food resources. The body mass of coexisting desert rodents seems to correspond to the partitioning of food resources by size and hardness (R.S. Miller 1964:259; J.H. Brown 1975). Among some kinds of birds, too, food size, rather than the food's taxonomic category, appears to be more important in determining what is eaten (Hespenheide 1971). Birds of very different body weights or bill sizes show considerable overlap in the sizes and types of prey that they eat (Wiens 1977:590). Their diets

vary through the season, but at a particular time the different species have a very similar diet, probably because birds respond opportunistically to the most abundant food.

Organisms sometimes compete for habitat. Observed body-size differences of various taxa in certain cases might primarily reflect microhabitat allocation, and only secondarily the allocation of food sizes. Species are likely to feed in different habitats if there are many competitors for a particular range of food sizes and it is impossible to partition food use by size (Schoener 1965). Size gaps in community arrays of shorebirds and waterfowl are attributed to interspecific aggression for limited habitat (Oksanen et al. 1979). There is, however, controversy over whether these gaps are real or merely the result of investigator bias (Nudds et al. 1981).

The second hypothesis is that differences in body size might be an evolutionary response to predation. Predation may sometimes be more important than competition in determining body sizes (Hairston 1980). But this would not explain a constant size difference throughout an array of species.

Third, dispersing organisms might encounter size-dependent causes of mortality. Some sizes might be better suited physically or behaviorally for survival in a new environment. Also, differential survival of immigrating species is likely to be determined by their distinctness from species already there (Grant 1969, 1970). Immigrants that are too similar to the resident species might fail to establish themselves. Immigrants that are ecologically different, however, are likely to have better success in surviving the hazards of dispersal and in establishing themselves in sympatry.

Fourth, hybrids usually are larger and more vigorous than either parent. Immigrants arriving in a new area are likely to be from different demes, and their surviving offspring are likely to be more vigorous and larger than either parent (J. Juan Spillett, pers. comm.).

Fifth, reproductive success under a particular set of environmental circumstances might be related to the parents' body size. Thus, many or all of the species being considered in a locality might exhibit character displacement (J. Juan Spillett, pers. comm.).

Sixth, morphological characters might vary geographically as a consequence of different nutrient availability, temperatures, or moisture. Variations are well known to occur across ecological, latitudinal, or longitudinal clines.

Seventh, morphological character differences might occur as a manifestation of mechanisms ensuring reproductive isolation. The character displacement which occurs when species coexist is possibly a consequence of a more rigorous selection for mates. An individual might select mates that are most like itself (Paterson 1980) or most different from the other species, i.e. a process to minimize hybridization resulting from mistaken identity (W.L. Brown and E.O. Wilson 1956; Grant 1972a).

Eighth, the observed size differences might be due to randomness (Strong et al. 1979). This possibility is often ignored in the ecological literature. The observed ratio, whatever it is, might be a chance occurrence.

Differences in morphological features resulting from any or all of the above eight causes can determine which species will persist in a community. Grant and Abbot (1980:336) emphasized the importance of

recognizing the distinctions.

Considerable disagreement still exists over how much effect competition has on community structure (Lewin 1983a, 1983b), but in some communities it clearly is important. Although ecology traditionally has stressed the role of competitive exclusion in explaining the structure of biotic communities, the emphasis has recently shifted to the search for a principle of limiting similarity (MacArthur and Levins 1967; May and MacArthur 1972). Natural selection would be expected to result in competing species differing by a minimum amount in their use of limited resources.

What is the functional significance of variations in body size? Among salamander species, the same ratios exist for their mean prey size as for their linear body measurements (Krzysik 1979). Among birds, the predator's body weight is a better predictor of prey size eaten than is any linear measure of the bill (Hespenheide 1971). North American Carnivora were investigated by Rosenzweig (1966), with the conclusion that there is a trend of increased food size with larger predator body size. Notable exceptions occur, and Rosenzweig (1966) suggests that coexistence can be further achieved by a poor competitor preying on a superior competitor. In a review of mammals, Clutton-Brock and Harvey (1983:657) concluded that the size of a species relative to other closely related species is a better predictor of food sizes or types selected than is absolute size. This seems true in spite of the conclusion that because mammalian body size scales their life-history parameters, their size should, therefore, be of central ecological importance (Western 1979). Ecological inferences from morphological data were reviewed by Hespenheide (1973).

Morphological character shifts in sympatry might not always occur, because organisms probably can substitute a non-evolutionary behavioral displacement for morphological displacement. Also, size differences might not always be possible because of limitations in structural strength (Schmidt-Nielsen 1975). Changes in feeding behavior (Pianka 1978:195) or hunting technique, which sometimes determine the prey size that can be taken (Enders 1975), might eliminate the need for physical changes. Behavioral character displacement appears to precede and substitute for morphological character displacement in the evolution of feeding habits of skinks (Huey and Pianka 1974). And avian species show substantial independence among foraging variables such as food type, feeding method, and habitat (Hutto 1981). Frugivorous birds show aggressive interference, and, thus, might be expected to feed at different times of the day, which in fact the most common species do, even though the food resource is not renewable (Kantak 1981).

What some species gain by growing larger or by behaving differently, other species can achieve by living in cooperative groups. African wild dogs live in packs year-round, and the entire pack usually cooperates in food getting (Malcolm and H. van Lawick 1975). Lions too hunt cooperatively, but the size of their hunting groups varies according to the available prey (Schaller 1972). The same flexibility of foraging-group size might apply to jackals (Lamprecht 1978a) and to a lesser extent to African wild dogs (L.H. and G.W. Frame, unpubl. data), although cheetah (G.W. Frame and L.H. Frame, in prep.) and leopard (Bertram 1978) hunting-group sizes are not affected by prey size. Spotted hyenas show the most flexibility in foraging-group size, essentially hunting independently, but feeding together when the prey

is large (Kruuk 1972a). A review of the literature by Griffiths (1980) concluded with the generalization that pack hunting enables capturing larger prey.

The validity of both the 2.0 body-weight rule and the 1.28 body-length rule has been questioned by Horn and May (1977), Roth (1981), and Simberloff (1983), although some researchers (e.g. Maiorana 1978) offer explanations of why the supposed constant ratios occur. Evidence failing to substantiate the hypothesized ratios is mounting. For example, in a study of bird guilds (Willson 1974:1021-1022), the mean weight ratio of the ranked guild members was between 1.7 and 4.0, the mean bill-length ratios were 1.1 to 1.6, and mean bill-depth ratios were 1.15 to 2.00. These vary widely from the hypothesized values. Also, a study of spider crabs concluded that the body-size linear ratios were larger than predicted (Hines 1982). After reviewing the evidence of character displacement, Grant (1972a) concluded that the phenomenon of differences in body size or in size of feeding apparatus appear to have occurred in insects, snails, lizards, birds, and mammals, but the evidence supporting the theoretical ratios is weak.

Circular reasoning and biased reporting of data have plagued the subject and prevented a better understanding of character displacement and the likelihood of predictable size ratios (Roth 1981). Apparent morphological character displacement in coexisting birds was tested against computer-generated random assemblages of birds, with the conclusion that no community-wide character displacement was detectable (Strong et al. 1979). Most of the studies purporting to show character displacement seem not in actuality to demonstrate anything distinct from a random assemblage (Strong 1980). Comparison of data from real

communities of birds with null communities formed in Monte Carlo fashion, however, showed significant size differences (Case et al. 1983). The controversy (cf. Grant and Abbott 1980; Hendrickson 1981; Strong and Simberloff 1981; Simberloff and Boecklen 1981; Case and Sidell 1983) continues.

13.2 The Tests

In the Serengeti ecosystem, 27 species of Carnivora (Table 13.1) and at least ten species of ungulate-eating birds (Table 13.2) coexist. The mammals show much behavioral plasticity in their use of foods and habitats, as well as in their diel activities (e.g. Lamprecht 1978b, 1981). Even though many of the Serengeti's Carnivora and scavenging birds feed substantially on the same foods, I initially analyzed them separately, because they are taxonomically so different. The capability of flight, especially, makes an immense difference in their ability to use the resources, because vast areas can be quickly searched from the air. Few species are cogeneric among the Serengeti's carnivorous mammals and birds, but the intent here is to ascertain whether or not there is a community-wide pattern of morphological character displacement.

The first analysis includes all Carnivora living in the Serengeti ecosystem (Table 13.1). Simberloff (1978:714) suggested examining data at the family level for evidence of competition, although Simberloff and Boecklen (1981) cautioned that this might obscure subtle points of interest. The Serengeti's Carnivora, however, show substantial competitive interactions among species of different families, and, therefore, seem appropriate for consideration at this high taxonomic

Table 13.1 Carnivora body weights and weight ratios in the Serengeti ecosystem.

Species of Carnivora[1]	Reference	Typical Weight (kilograms)[2]	Ratio[3]
Dwarf mongoose	4, 5	0.3	
			1.33
Slender mongoose	6	0.4	
			3.00
Zorilla	6	1.2	
			1.00
Banded mongoose	6	1.2	
			1.25
Common genet	6	1.5	
			1.00
Large-spotted genet	4	1.5	
			1.80
Bat-eared fox	7	2.7	
			1.04
Marsh mongoose	8	2.8	
			1.07
Egyptian mongoose	6	3	
			1.33
African wild cat	6	4	
			1.00
White-tailed mongoose	4	4	
			1.63
Ratel	6	6.5	
			1.23
Aardwolf	6	8	
			1.00
Side-striped jackal	6	8	
			1.25
Serval	6	10	
			1.00
Caracal	6	10	
			1.10
Common jackal	9	11	
			1.00
Black-backed jackal	9	11	
			1.00
Two-spotted palm civet	8	11	
			1.09
African civet	6	12	
			1.50

(continued on next page)

(Table 13.1, continued)

Cape clawless otter	8	18	
			1.11
African wild dog	6, 10	20	
			1.30
Striped hyena	11	26	
			1.73
Leopard	12	45	
			1.02
Cheetah	13	46	
			1.13
Spotted hyena	14, 15	52	
			3.06
Lion	15, 16, 17, 18	159	

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1 Arranged in sequence of increasing adult body weight; scientific names are in Appendix B.
2 Weights derived from means, medians, and estimates of males and females combined.
3 Ratio between adjacent species in the ordered sequence.
4 Hendrichs (1972).
5 Rood (1983).
6 Hendrichs (1970).
7 Lamprecht (1979).
8 Dorst and Dandelot (1970); these weights were used when none was available from the Serengeti ecosystem.
9 Moehlman (1983).
10 L.H. and G.W. Frame, unpubl. data.
11 Kruuk (1976).
12 Bertram (1982).
13 G.W. Frame and L.H. Frame, in prep.
14 Kruuk (1972a:211).
15 L.M. Talbot and M.H. Talbot (1961).
16 Schaller (1972:30, 210).
17 Sachs (pers. comm., cited in Schaller 1972:30).
18 Bertram (1978).

Table 13.2 Scavenging-bird body weights and weight ratios in the Serengeti ecosystem.

Species of Scavenging Bird[1]	Body Weight (kilograms)[2]	Ratio[3]
Black kite	0.8	
		1.13
White-necked raven	0.9	
		2.00
Egyptian vulture	1.8	
		1.03
Hooded vulture	1.85	
		1.03
Tawny eagle	1.9	
		1.32
Bateleur	2.5	
		1.80
White-headed vulture	4.5	
		1.22
Marabou	5.5	
		1.07
African white-backed vulture	5.9	
		1.12
Lappet-faced vulture	6.6	
		1.17
Rüppell's vulture	7.5	

1 Arranged in sequence of increasing body weight; scientific names are in Appendix B.
2 Weights adapted from Houston (1975b, 1976, 1979, 1980) and C.J. Pennycuick (1971).
3 Ratio between adjacent species in the ordered sequence.

level. The data sets to be analyzed were selected because of their completeness and relevance to feeding competition. Body weights in the Serengeti ecosystem are available for all the Carnivora (Table 13.1). Mammalian weights vary substantially from area to area (Sachs 1967; Kruuk 1972a:211), so only body weights typical of the Serengeti ecosystem are used in the analysis. Linear measurements for Serengeti ecosystem Carnivora are incomplete, so their use is precluded.

The second analysis is of the scavenging birds (Table 13.2). Among the vultures and other large carnivorous birds, competition apparently is reduced by character displacement and by behavioral specializations on food parts and sequence of feeding (Petrides 1959; Kruuk 1967). Seven of the 11 bird species feed mainly or entirely on carrion (Houston 1979), and the last four species in Table 13.2 account for about 98% of the meat consumed by the scavenging birds (Houston 1980). Morphological, behavioral, and ecological features of these birds are discussed in Kruuk (1967) and Houston (1979, 1980). The vulture linear measures are skull length (Table 13.3), skull width (Table 13.4), bill length (Table 13.5), and bill width (Table 13.6). The typical species weight and linear measurements used here are of adults only and approximate an average of the two sexes.

The third analysis is of the ungulate-eaters (Table 13.7). Defining a meaningful group for analysis is a fundamental problem, because adding extra species can make an apparent size pattern disappear (A.E. Chew and R.M. Chew 1980). The problems involved in deciding which sympatric species, sexes, or ages to compare, and which measures to use in comparing them, were reviewed by Wiens (1982).

Table 13.3 Vulture skull lengths and skull-length ratios in the Serengeti ecosystem.

Species of Vulture[1]	Skull Lengths (millimeters)[2]	Ratios[3]
Egyptian vulture	108	
		1.01
Hooded vulture	109	
		1.19
White-headed vulture	130	
		1.00
African white-backed vulture	130	
		1.11
Rüppell's vulture	144	
		1.03
Lappet-faced vulture	149	

1 Arranged in sequence of increasing skull length.
2 Measurements from Kruuk (1967).
3 Ratio between adjacent species in the sequence.

Table 13.4 Vulture skull widths and skull-width ratios in the Serengeti ecosystem.

Species of Vulture[1]	Skull Widths (millimeters)[2]	Ratios[3]
Hooded vulture	47	
		1.02
African white-backed vulture	48	
		1.04
Egyptian vulture	50	
		1.08
Rüppell's vulture	54	
		1.30
White-headed vulture	70	
		1.16
Lappet-faced vulture	81	

1 Arranged in sequence of increasing skull width.
2 Measurements from Kruuk (1967).
3 Ratio between adjacent species in the sequence.

Table 13.5 Vulture bill lengths and bill-length ratios in the Serengeti ecosystem.

Species of Vulture[1]	Bill Lengths (millimeters)[2]	Ratios[3]
Egyptian vulture	57	
		1.02
Hooded vulture	58	
		1.07
White-headed vulture	62	
		1.06
African white-backed vulture	66	
		1.15
Rüppell's vulture	76	
		1.05
Lappet-faced vulture	80	

1 Arranged in sequence of increasing bill length.
2 Measurements from Kruuk (1967).
3 Ratio between adjacent species in the sequence.

Table 13.6 Vulture bill widths and bill-width ratios in the Serengeti ecosystem.

Species of Vulture[1]	Bill Widths (millimeters)[2]	Ratios[3]
Egyptian vulture	9	
		1.22
Hooded vulture	11	
		1.91
African white-backed vulture	21	
		1.10
White-headed vulture	23	
		1.00
Rüppell's vulture	23	
		1.39
Lappet-faced	32	

1 Arranged in sequence of increasing bill width.
2 Measurements from Kruuk (1967).
3 Ratio between adjacent species in the sequence.

Table 13.7 Ungulate-eating carnivore body weights and weight ratios in the Serengeti ecosystem.

Carnivore Species[1]	Body Weights (kilograms)[2]	Ratios[3]
Egyptian vulture	1.8	
		1.03
Hooded vulture	1.85	
		1.03
Tawny eagle	1.9	
		2.37
White-headed vulture	4.5	
		1.22
Marabou stork	5.5	
		1.07
African white-backed vulture	5.9	
		1.12
Lappet-faced vulture	6.6	
		1.14
Rüppell's vulture	7.5	
		1.47
Asiatic jackal	11	
		1.00
Black-backed jackal	11	
		1.82
African wild dog	20	
		2.25
Leopard	45	
		1.02
Cheetah	46	
		1.13
Spotted hyena	52	
		3.06
Lion	159	

1 Arranged in sequence of increasing body weight.
2 Weights from Tables 13.1 and 13.2.
3 Ratio between adjacent species in the sequence.

The Serengeti's carnivore data are examined for possible fit to predicted patterns of size differences in morphological characters. If the predicted spacing patterns are found, it would be remarkable support for an ecological principle that predictable size differences occur in competitive communities even where other (non-morphological) kinds of character shifts are occurring. Because many exceptions are known elsewhere from published studies, Serengeti carnivore support for the hypothesized mathematical relationships might aid in restating the problem in more precise terms. If predictable spacing patterns are not found, there still is value in reporting the negative results to balance the argument (cf. Simberloff and Boecklen 1981:1223).

The Serengeti data are compared with the two most commonly hypothesized patterns of spacing that are expected to occur along one-dimensional resource axes; these are uniform and geometric. The statistical tests for these different patterns of separation to be used here were described by Poole et al. (1979) and Poole and Rathcke (1979). End points of the size axis were defined by the smallest and largest measurements in the series, with a loss of two degrees of freedom. The mean of the observed ratios is used as the constant of multiplication in testing for a geometric relationship. Their null hypotheses state that there are no differences between the observed distributions and randomness on the pattern tested. One-tailed tests are used. The corresponding alternative hypotheses are that the observed distributions are different from the specified patterns.

13.3 Results

13.3.a Carnivora

Calculated body-weight ratios for the ordered 27 species of Serengeti ecosystem Carnivora (Table 13.1) range from 1.00 to 3.06 (mean = 1.35, median = 1.12). The null hypothesis that the observed body weights do not differ from a random uniform pattern was rejected ($df = 25$, t.s. = 12.23, $p << 0.005$). Because the pattern is therefore different from uniform, i.e. the data are highly aggregated, the next test was for a geometric pattern. The null hypothesis that the observed body weights do not differ from a random geometric pattern was rejected ($df = 25$, t.s. = 14.53, $p << 0.005$). Thus, the Serengeti Carnivora body-weight ratios show neither a uniform nor geometric pattern.

13.3.b Scavenging Birds

Calculated body-weight ratios for the ordered 11 species of Serengeti ecosystem scavenging birds (Table 13.2) range from 1.03 to 2.00 (mean = 1.29, median = 1.15). As for the Carnivora, the birds' ordered weight ratios were tested for two patterns of spacing. The null hypothesis that the observed body weights do not differ from a random uniform pattern (sensu Poole et al. 1979) was rejected ($df = 9$, t.s. = 85.96, $p << 0.005$). The null hypothesis that the observed body weights do not differ from a random geometric pattern also was rejected ($df = 9$, t.s. = 2.92, $p < 0.005$). Thus, the Serengeti scavenging-bird body-weight ratios show neither a uniform nor geometric pattern.

Four linear skull measurements are available for six species of Serengeti vultures (from Kruuk 1967:179). Data are unavailable for the marabou stork and tawny eagle. Measurements of vultures for the features of interest are arranged in order of increasing size in each of the following four ways:

(1) Skull-length ratios (Table 13.3) ranged from 1.00 to 1.19 (mean = 1.07, median = 1.03). The null hypothesis that the observed linear measurements do not differ from a random uniform pattern was not rejected (df = 4, t.s. = 1.46, p = 0.27).

(2) Skull-width ratios (Table 13.4) ranged from 1.02 to 1.30 (mean = 1.12, median = 1.08). The null hypothesis that the observed linear measurements do not differ from a random uniform pattern was not rejected (df = 4, t.s. = 1.89, p = 0.10).

(3) Bill-length ratios (Table 13.5) ranged from 1.02 to 1.15 (mean = 1.07, median = 1.06). The null hypothesis that the observed linear measurements do not differ from a random uniform pattern was not rejected (df = 4, t.s. = 0.61, p = 0.68).

(4) Bill-width ratios (Table 13.6) ranged from 1.00 to 1.91 (mean = 1.32, median = 1.22). The null hypothesis that the observed linear measurements do not differ from a random uniform pattern was not rejected (df = 4, t.s. = 1.18, p = 0.37).
Consequently, each of the four sets of linear measurements for vulture skulls or bills shows a uniform pattern.

Frequency distributions of ratios from the four linear measurements of vultures are shown in Figure 13.1. Linear measurements as a function of body weight for the six species of vulture are plotted in Figure 13.2. Using the order of increasing body length, rather than

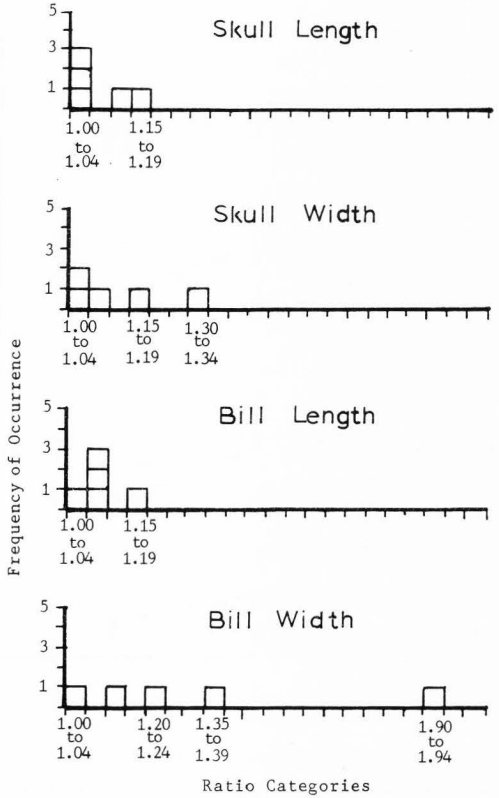

Figure 13.1 Frequency distributions of linear-measurement ratios among six species of vulture in the Serengeti ecosystem. The ratios are from Tables 13.3, 13.4, 13.5, and 13.6.

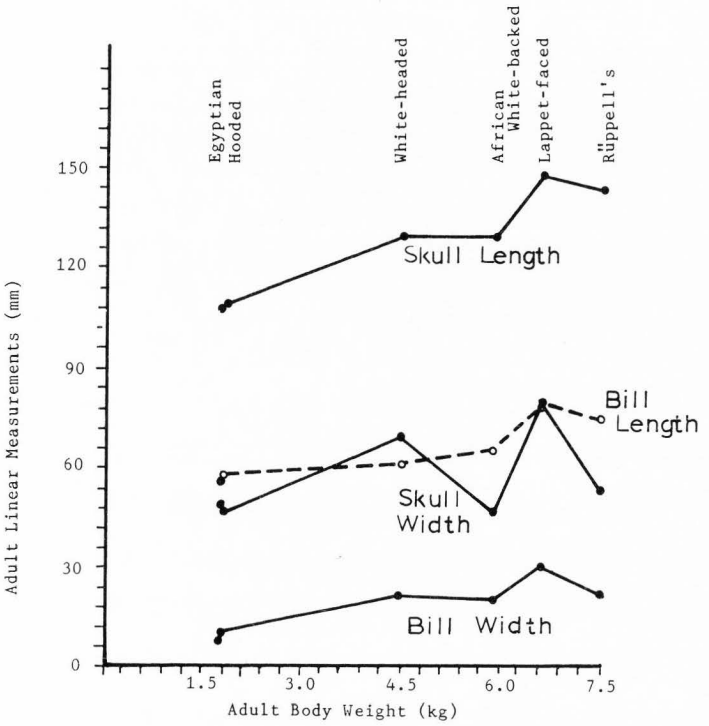

Figure 13.2 Body-weight and linear-measurement relationships among six species of vulture in the Serengeti ecosystem. Data are from Tables 13.2 and 13.8.

the increasing size of the one feature being considered, the ratios are again calculated (Table 13.8). The result is that there still are unpredictable ratios, with a wide range of values.

13.3.c Ungulate-eaters

Body weights and weight ratios for the ordered 15 species of the Serengeti ecosystem's ungulate-eaters are shown in Table 13.7. The ratios range from 1.00 to 3.06 (mean = 1.48, median = 1.14). The ordered body weight ratios were tested for uniform and geometric spacing. The null hypothesis that the observed body weights do not differ from a random uniform pattern was rejected ($df = 13$, t.s. = 6.83, $p << 0.005$). The null hypothesis that the observed body weights do not differ from a random geometric pattern also is rejected ($df = 13$, t.s. = 6.27, $p << 0.005$). Thus, the Serengeti ungulate-eater body-weight ratios show neither a uniform nor geometric pattern.

Frequency distributions of body-weight ratios for each of the three carnivorous animal groups are shown in Figure 13.3.

13.4 Discussion

Morphological character differences occur in unpredictable ways among the Serengeti ecosystem's carnivorous birds and mammals. No widespread pattern of uniform or geometric spacing of body weights was found.

The distribution of ordered body-weight ratios (Figure 13.3) appears to be closer to uniform among the 15 ungulate-eaters than in either the Carnivora or the scavenging birds, but still it is not uniform. This might be an artifact of combining two taxonomic classes,

Table 13.8 Vulture skull and bill linear measurements, arranged in order of increasing body length of the species. Data are from Kruuk (1967:179). Ratios are between adjacent species in the body-size sequence.

Species of Vulture	Skull Greatest Lengths (mm)	Ratios	Skull Greatest Widths (mm)	Ratios	Bill Lengths (mm)	Ratios	Bill Widths (mm)	Ratios
Egyptian	108		50		57		9	
		1.01		0.94		1.02		1.22
Hooded	109		47		58		11	
		1.19		1.02		1.14		1.91
African white-backed	130		48		66		21	
		1.00		1.46		0.94		1.10
White-headed	130		70		62		23	
		1.11		0.77		1.23		1.00
Rüppell's	144		54		76		23	
		1.03		1.50		1.05		1.39
Lappet-faced	149		81		80		32	

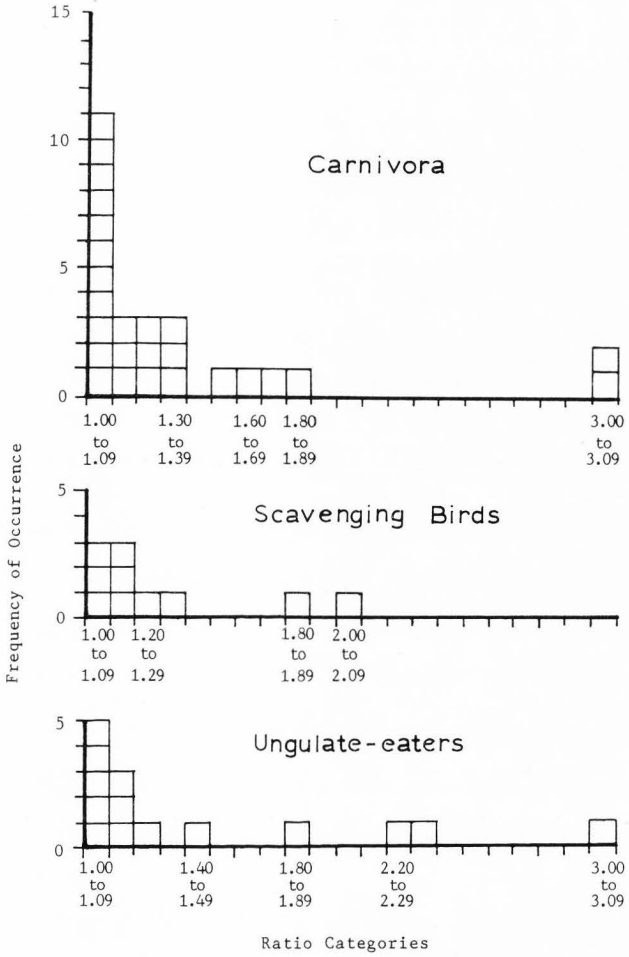

Figure 13.3 Frequency distributions of body weight ratios among carnivorous mammals and birds in the Serengeti ecosystem. The ratios are from Tables 13.1, 13.2, and 13.7.

i.e. two very different animal assemblages mixed together might be expected to have more species pairs with large body-weight ratios. In contrast, the high aggregation of body-weight ratios among the 27 species of Carnivora and among the 11 species of scavenging birds shows that most of the coexisting, ordered species pairs are very similar in size within each taxon. Presumably the coexistence of so many similar-sized animals is possible because of their very diverse uses of foods and other resources. Among the ungulate-eaters the common use of essentially one food resource could be permitted by a greater disparity of carnivore body sizes and feeding behaviors.

Within a small group of closely-related animals, namely the six species of vultures, skull and bill lengths or widths were uniformly spaced. Examination of small groups of other closely-related species--e.g. the mongooses, the felids, or the canids--might show similar patterns. Simberloff and Boecklen (1981) reported that the tests described by Barton and David (1956) are more sensitive to non-randomness than are the Poole et al. (1979) tests, so further testing of the Serengeti data should consider the Barton and David tests. Given enough genetic diversity and evolutionary time, parsimony suggests that body weights and lengths are randomly, but approximately uniformly distributed throughout the entire possible size range. This most-simple pattern might be postulated to occur in both the non-competitive and competitive situations, depending upon the distribution of resources. The randomly-uniform patterns (sensu Poole et al. 1979) of displaced, linear morphological characters in vultures is parsimonious and can be argued as being evidence either for or against an evolutionary response to competition.

Body weights, body lengths, and the size of structures important for feeding vary in an inconsistent manner (Figs. 13.2 and 13.3). Species ordered by linear measurements are most widely spaced in their bill-width ratios (Fig. 13.1). Kruuk (1967) categorized the Serengeti vultures into three groups according to their feeding behavior; they are: (1) Egyptian and hooded, (2) white-headed and lappet-faced, and (3) African white-backed and Rüppell's. They often are in competition (cf. Section 10.2.h). Neither similarity of body weight nor similarity of linear measurements is a good predictor of which species feed on the same food resources (Fig. 13.2).

Both the community-wide view and the more restricted similar-species view of the Serengeti carnivores generally failed to confirm the hypothesized geometric patterns of character displacement. To some extent these results support Simberloff's (1983) conclusion that the sizes of coexisting species generally are not a coevolutionary result of interspecific competition. Regardless of whether other patterns of aggregation exist or not, the results agree with Strong et al. (1979) and Strong (1980) in that much of the size variation is probably of stochastic origin. The effects of clinal variations, hybridization, differential reproductive success, reproductive isolation, and differential survival from predation and dispersal must also enter into the explanation. Further analyses of ratio data, as was done by Roth (1981), would be of questionable value, because statistical properties of the data are changed when ratios are formed (Atchley et al. 1976). Thus, there is no convincing support from the Serengeti data that character displacement is an evolutionary response to competition, at least not in the predicted geometric manner.

Another avenue of investigation is to consider the 0.75-power relationship that exists between body weight and energy requirements (J. Juan Spillett, pers. comm.). This would provide a more logical size-difference relationship than the hypothesized geometric 2.0 and 1.28 ratios. A test for regular exponential patterns was described by Poole et al. (1979).

CHAPTER XIV

CONCLUSIONS

In the preceding chapters I tried several approaches to describing and understanding how the many ungulate-eaters coexist in the Serengeti ecosystem. The present chapter draws together what was learned from those analyses. Section 14.1 assesses the importance of competition among the Serengeti carnivores at both the individual and population levels. Evolutionary consequences of the interactions are considered in Section 14.2. Wildlife management then is addressed in Section 14.3, by discussing the usefulness of the methods that I used. In Section 14.4 I suggest a management strategy for the Serengeti carnivores.

14.1 Importance of Competition for Serengeti Carnivores

There is scant evidence of exploitation competition in the Serengeti carnivores. There is occasional starvation of offspring that are too young to travel, e.g. lions (Schaller 1972:183, his Table 31), spotted hyenas (Kruuk 1972a), and African wild dogs (G. and L. Frame 1981). Adult cheetahs might also starve during unusually bleak conditions (H. van Lawick, pers. comm., cited in G.W. Frame and L.H. Frame, in prep.). When starvation does occur, it is due to the inequitable distribution of the ungulate prey in the ecosystem. Waser (1981, 1985) studied the influence of resource renewal on the spacing patterns of the Serengeti's small Carnivora. This subject, however, has been dealt with less directly by the numerous researchers who

studied the larger Carnivora.

At first glance in Table 2.2, the Serengeti's ungulate-eaters seem to have a huge food resource in the ecosystem, numbering over three million ungulates (excluding hyraxes, cf. Appendix A). But, when calculated on a per capita basis from Tables 2.1 and 2.2, there are only 55 ungulates in the standing crop per ungulate-eating mammalian predator. Or, if hyraxes are included among the ungulate prey, there are 93 ungulates standing crop per ungulate-eating mammalian predator. In view of the uneven and unpredictable spatial distribution of the prey, the food supply might indeed be limiting at times. As supplies of resources begin to diminish, aggressive encounters increase, e.g. the increased aggressiveness by spotted hyenas against African wild dogs in the dry season (cf. Section 9.2.a). Interference competition between individuals of two species is a commonly reported phenomenon in the Serengeti ecosystem (Chapter Ten). Two important aspects of interference competition are cleptoparasitism and killing other carnivores. The increased costs incurred by the inferior competitor in these aggressive and predatory interactions range from slight to severe.

Cleptoparasitism occurs openly and is the easier kind of interference competition to observe. Lions and spotted hyenas readily appropriate prey caught by cheetahs, African wild dogs, and other smaller carnivores. The energy cost to the carnivores which lose these meals, however, appears to be slight when considered over their entire lifetime. For example, cheetahs lose only about 10% of their meals year-round to lions, leopards, and spotted hyenas (Schaller 1972; G. and L. Frame, in prep.), and this often is after the cheetah has

eaten part of the prey. African wild dogs lose perhaps even less to lions and spotted hyenas (Estes and Goddard 1967; L.H. and G.W. Frame, unpubl. data). Lions, because they are highly social as well as the largest carnivore in the Serengeti ecosystem, are less vulnerable to losing food to other large predators, except to the spotted hyena. Lions also experience some losses to the much smaller jackals and vultures (Schaller 1972; Kruuk 1972a; Bertram 1978). Leopards are very secretive, and their superb ability to carry food high into the trees prevents large losses to other carnivores (Schaller 1972; Bertram 1978). When viewed year-round throughout the ecosystem, these interspecific food losses do not appear to be an important cause of mortality or decreased reproduction in the populations of Carnivora.

Killing individuals of other carnivore species is the second form of interference competition. Sometimes animals are killed directly for a food resource, although more often it appears to be the consequence of social intolerance. Social intolerance, however, also is the result of competition for resources. Often the individuals of the competing species seem to regard each other as conspecifics rather than as prey. Other times, the victim is killed and at least partially eaten, so the motive for killing is unclear. Predation among carnivores can allow a competitor to successfully invade a community (Powell and Zielinski 1983). Leopards apparently use the other Carnivora for food quite often (Section 10.2).

There are no quantitative data on the frequency of interspecific killing. But it appears to me that interspecific killing is an important population constraint on many of the Serengeti Carnivora. When resources are limited, it is the resulting aggression or predation

which is the apparent mortality cause rather than resource limitation *per se*. Since exploitation competition and cleptoparasitism, although exerting some influence, appear not to be very important, it is interspecific killing which probably remains the most influential mode of interspecific competition for both individuals and populations. Population suppression as a consequence of interspecific killing also appears to occur among North American Carnivora (e.g. F.H. Wagner 1975:5).

Both forms of interference competition--cleptoparasitism and killing--also occur within species. All of the more thoroughly studied species of large and medium-sized Carnivora show examples of intraspecific killing. This occurs in lions (Schaller 1972; Bertram 1978; Bygott et al. 1979; Packer and Pusey 1982), spotted hyenas (Kruuk 1972a), cheetahs (G. and L. Frame 1981), and African wild dogs (L.H. Frame et al. 1979; G. and L. Frame 1981).

Nearly all the interspecific competition examples in the Serengeti ecosystem are effects on individuals rather than on populations. Competition's consequences at the population level, as numerical responses, are difficult to generalize because long-term population data for most of the carnivores are lacking. However, in two localities--the Serengeti Plains and the Ngorongoro Crater--there are sufficient long-term data to show population trends in lion (Hanby and Bygott 1979; Bygott and Hanby 1977), spotted hyena (Serengeti Research Institute 1977a, 1977b), and African wild dog (Section 9.2.a). The evidence of a suppression effect is strongest for the African wild dog as discussed in Sections 9.2.a and 10.2.e. The only evidence for the other ungulate-eaters is described in Section 10.2.

Despite the paucity of evidence, it seems likely that population suppression is a common phenomenon among the Serengeti's Carnivora, but varying in importance among species. Unlike populations of animals in temperate climates, where abiotic factors such as harsh weather are responsible for considerable mortality (e.g., cf. F.H. Wagner and Stokes 1968), the Serengeti Carnivora appear to be nearly free of such constraints. Starvation and disease appear to be only minor causes of mortality, except when they are the direct result of interference competition. The probable remaining constraints are interspecific and intraspecific interactions. As we have seen, the former is the significant force operating on the African wild dog and perhaps the cheetah. In the absence of interference competition and predation, their populations would probably increase up to the point where intraspecific interference competition would intensify and eventually prevent further population increase. Lion and spotted hyena, by virtue of their size and robustness, are probably less influenced by interspecific forces and may already have increased to densities where the consequences of their own behavior is the primary population constraint (cf. Hanby and Bygott 1979; Kruuk 1972a).

The several models of community structure that were examined in Chapter Twelve were not supported by the Serengeti ungulate-eating Carnivore data. Even though competition seems to affect the carnivore community structure in the Serengeti ecosystem, it does not do so in all the predicted proximate ways. For instance, contrary to predictions of the models discussed in Chapter Twelve, Serengeti carnivores have larger food-niche breadths and overlaps in varying and unpredictable environments, which are the kinds of situations where

interference competition is greatest. The range of food types utilized by cheetahs and African wild dogs is greater when interference competition is less, although the deciding factor might be that more food types are eaten because of their plentiful availability. Food generalists, viz. spotted hyenas, outcompete the specialists, e.g. cheetahs and African wild dogs, although they do so by interference rather than by exploitation competition.

14.2 Evolutionary Considerations

Animal demes in the Serengeti ecosystem are highly connected in the sense that they affect one another intricately, both within and among species (cf. Chapter Ten). As such, the carnivores probably are coevolving. McNaughton (1979a) described the intense interactions that occur among the Serengeti's plants and the herbivores that graze them, and concluded that there must be substantial evolutionary effects. A similar intensity of coevolution is occurring between the carnivores and their prey, and among the carnivores themselves. These latter interactions seem to be support for the Red Queen hypothesis (reviewed by Lewin 1985), which states that the most important components of a species' environment are other species, rather than physical factors. The coevolution that is occurring, however, is not affecting the body weights and sizes of the carnivores in the predicted manner (cf. Chapter Thirteen).

Although individuals are the organismic units that are doing the competing, some accompanying group selection could occur (e.g. D.S. Wilson 1980:20), but this remains in debate (e.g., cf. Krebs and Davies 1981:249-252). The non-related lion or cheetah males that cooperate to

defend a territory, and thereby improve their genetic fitness (Packer and Pusey 1982; G. and L. Frame 1981), can be explained by individual selection alone. Individuals increase their relative fitness by interacting with conspecifics in their local population.

If aggressive behavior has a genetic component, the result should be a directed gene-frequency change in the deme. Conspecifics sometimes kill for a limited resource, such as preferred habitat or a mate. The more-aggressive competitor successfully reproduces at the expense of his opponent. Even while some kin lines may be outstandingly successful in producing progeny, the population of which they are all a part can be evolving toward extinction (W.D. Hamilton 1971; Roughgarden 1976; both cited in D.S. Wilson 1980:16).

J.D. Thomson's (1980) article about the implications of different kinds of evidence of competition has contributed immensely to eliminating the confusion surrounding this subject. Thomson explained competition as a multi-faceted concept, with different properties depending on the chosen definition of competition and the evidence used to demonstrate it. He summarized the two main criteria for demonstrating the existence of competition as being numerical responses and niche shifts. Importantly, numerical changes and niche shifts are not necessarily equivalent, and shifts in niches need not affect community structure and species diversity.

Niche shifts are of two kinds: evolutionary shifts, such as character displacements, and nonevolutionary shifts, such as behavioral changes (Thomson 1980). The tests for patterns of character displacement among the Carnivora and ungulate-eating birds in the Serengeti ecosystem show that the hypothesized uniform and geometric

morphological relationships do not exist (Chapter Thirteen), except in limited cases. Behavioral shifts probably substituted for the predicted shifts in body weight and size in the competitive carnivore community. An individual often can easily compensate for its morphological inadequacies by changing its behavior. Behavioral flexibility is a vital asset.

Coexistence in other communities of Carnivora is dependent on many factors besides body-size differences that allow feeding on different food sizes. In mustelid communities, for example, important niche separations--probably both evolutionary and non-evolutionary--result from differences in prey taxa, habitats, and hunting methods (reviewed in Powell and Zielinski 1983). Red foxes (Vulpes vulpes) and grey foxes (Urocyon cinereoargenteus) in Maryland, U.S.A., have overlapping feeding habits but different diets (Hockman and Chapman 1983). In some localities of India, by comparison, wolves (Canis lupus), jackals, hyenas, domestic dogs, and leopards coexist on diets of goats, pigs, and smaller mammals and birds (Shahi 1983). Many other examples of coexisting and coevolving species are reviewed in D.S. Wilson (1980), Pontin (1982), J.N. Thompson (1982), and Futuyma and Slatkin (1983). While coexistence is usually considered to be perpetuated through differential exploitation of resources, the Serengeti ecosystem's carnivores seem to be remarkably similar in important ways (Chapters Four and Five). The Serengeti's carnivores apparently are able to coexist, in part, because of the unpredictability of the environment and their behavioral flexibility.

The long term variation in dry-season rainfall in the Serengeti (described by Hanby and Bygott 1979) seems to parallel the situation

among shrub-steppe birds in North America (Wiens and Rotenberry 1979) in which intense competition occurs at intervals of several generations. Many factors keep ecological systems from reaching the equilibrium point permitted by the resources (Wiens 1977). The intense cleptoparasitism on African wild dogs by spotted hyenas in the dry seasons of the mid-1970's (Section 9.2.a) seems to be a good example of this phenomenon.

In conclusion, the effect of competition among carnivores in the Serengeti ecosystem is reduced by proximate behavioral adjustments. In a varying and unpredictable environment such as the Serengeti Plains, it probably is more important to remain behaviorally flexible than to evolve greater morphological separation. The selective forces of intraspecific competition probably in some cases are operating in opposition to the selective forces of interspecific competition.

14.3 Reflections on the Methodology

The various methods that I used in my analyses, the manner in which they were performed, and the quality of their results require further discussion. This section, therefore, is my assessment of them.

There is a problem with the quality of the data that were used in some of the niche descriptions. Some data were collected in a consistent manner for all the carnivore species in the comparison, viz. Sections 4.2, 4.5, 4.7, 4.8, 5.2 (first analysis), 7.2, 7.3, 7.5, 7.6, and 11.2 However, other comparisons had to use data from several sources, and those data were sometimes collected in slightly different ways and with different sampling intensities, viz. Sections 4.3, 4.4, 4.6, 5.2 (second analysis), 7.4, 8.2, 8.3, 8.4, and 8.5. Future

collections of resource-use data from all the ungulate-eaters should be performed in a consistent manner.

Where cluster analyses and niche-metrics calculations were performed on data representing more than one niche axis, marginal totals of the data matrices were used rather than the original multidimensional data (cf. Sections 3.2.b and 3.2.c). These projections onto the resource axes resulted in a loss of information, but greatly simplified the analyses. In the cluster analyses there is no way of assessing how much the object similarities were changed, short of rerunning the analyses using the original multivariate data and comparing the results with those obtained by using marginal totals. But this would involve several hundred thousand possible resource states, thousands of which were occupied. The same is true for the calculations of niche breadths and overlaps, i.e., results of analyses using the original multivariate data would have to be compared to the results obtained by using marginal totals.

Another approach was taken to assess how much distortion resulted from using marginal totals of the data matrices to calculate metrics of multidimensional niches. For this I recalculated the breadth and overlap of each axis separately, thereby avoiding the use of marginal totals. Then I combined the single-axis metrics by multiplication and by addition to obtain multi-axis metrics (Section 3.2.c). Comparisons of the projection, product, and summation methods show that the trends from widest to narrowest niche breadths and from greatest to least niche overlaps generally are similar for the three methods. However, within each series, reversal of one or more adjacent species or species pairs was common when the three methods were compared (Tables 4.5, 4.6,

4.8, 4.9, 5.1, 5.2, 7.3, 7.4, 11.1, and 11.2). Sometimes a species or species pair was ranked at opposite extremes by the projection method compared to the product and summation methods (Tables 5.1 and 5.2). It appears that the results of the product and summation methods are more similar to each other than they are to the projection method. In the future, a comparison of the results of the Colwell niche program run on the original multivariate data should be made with the results of these three short-cut methods.

The resource-use data, when statistically significant, were plotted as histograms. I feel that these comparisons are more useful for my purposes than are the multivariate results of the cluster analyses and niche metrics. The graphs show where the similarities are greatest on each individual niche axis. In the univariate comparisons, however, clustering, niche metrics, and graphs seem about equally useful for identifying similarities.

I chose an alpha level of 0.01 for the statistical tests, because of the multiple testing. This lessened the chance of making a type II error, but it also caused me to fail to reject a null hypothesis, when it would have been rejected at the $p = 0.05$ level. In the case of resource-use graphs (Section 3.2.d and Chapters Four, Five, Seven, Eight, and Eleven), I did not want to consider a particular niche axis unless there was a very high confidence that a real difference exists on that axis. And in testing community models (Section 3.6 and Chapters Twelve and Thirteen), I did not want to add support to a hypothesis unless there was very high confidence that the Serengeti data do indeed support it. Nothing was to be gained by accepting a less-stringent p-value.

The predictability (sensu Colwell 1974) of an environment depends upon constancy and contingency within that environment. Rainfall varies throughout the year in the Serengeti ecosystem. The differential availability of forage among various parts of the ecosystem is the reason for the annual migration of ungulates. The Serengeti Plains and many other areas of the ecosystem undergo more than a ten-fold change in ungulate densities throughout the year (Section 6.2). However, the Ngorongoro Crater, because of its abundant permanent water and forage, has nearly-constant ungulate numbers. Within any season at any location, isolated rain storms result in patchy renewal of forage, with a consequent patchy distribution of prey. The Serengeti carnivores, therefore, live in an unpredictable environment, because their supply of food varies by season and is contingent upon local movements by the ungulates. The Ngorongoro Crater is sufficiently small (cf. Section 2.4.b) that the carnivores are always near their food. On the Serengeti Plains, the distances are much greater (Section 2.4.a). There the carnivores, especially the non-breeding individuals, follow the prey to some extent, but eventually many carnivores are stranded without much food. Thus, any study of the Serengeti ecosystem's carnivore community must do so in the context of the predictability of the environment.

In the Serengeti's unpredictable environment, the occurrence and intensity of competition is highly variable. This is because resource use by the carnivores varies by time and by location (Chapters Seven and Eight). Nevertheless, competition is pervasive (Chapters Nine and Ten) and must be a major factor in community dynamics. I believe that a better understanding of the mechanisms at work in the carnivore

community will come from future study of simultaneous population changes among carnivores and ungulates with regard to environmental variables. Direct observations of individuals will show when and why exploitation competition and interference competition are important.

The community models that I tested (Chapters Twelve and Thirteen) should be retested when better data are available. My failure to confirm any of the hypotheses with the Serengeti carnivore data does not necessarily mean that the hypotheses are incorrect; only that they cannot be confirmed with the data at hand. If future data for all the ungulate-eating carnivores are collected in a consistent manner for the purpose of testing these models, the results might be different. I expect that the niche-breadth-variation hypothesis will eventually be confirmed by the Serengeti data (cf. Section 12.2).

Much of the Serengeti ecosystem is protected by the status of national park, conservation area, and game reserve. As a result, experimentation generally is forbidden by policy. In other areas of East Africa, where experimental manipulation of the fauna and flora might be permitted, it is unlikely that adequate ecological studies have been done to provide a baseline for experimentation. In such a situation the inadequate understanding of background conditions probably would render the results of experimental manipulations highly suspect, because of the inability to control, or even to recognize, all the important variables. For this reason, and for ethical reasons, I recommend that future research should be directed to continued monitoring and measurements in the best-studied systems, to refine our understanding of the natural processes that are occurring there.

14.4 Usefulness of Assessment Methods for Management

The earlier chapters about competition and niche relations are largely descriptive. Their primary value lies in the understanding they provide about the behavior and ecology of carnivorous species in a dynamic community--an assemblage in which the large and medium-sized Carnivora and avian scavengers repeatedly come into competition. Later chapters on non-evolutionary and evolutionary community models search for explanations of the observed phenomena. The purpose of this section is to examine how useful the niche descriptions and selected community models are in providing management insights for the Serengeti's wildlife.

Resources used by the carnivores were not all recognizable or measurable. Thus, practicality and observer subjectivity influenced the nature of the study. Most observers would agree, however, that food and habitat are very important for all carnivores. Fortunately, these two resources are among the easiest to measure. In assessing relationships among the Serengeti ecosystem's Carnivora, temporal and locational effects also were considered.

I used three methods to describe niche relationships--cluster analyses, niche breadths and overlaps, and graphical comparisons--to identify the carnivores that are most similar in resource use. Interspecific niche studies usually focus on a community of many different species, with each niche representing an investigator-defined population of one species. This is the context in which they were used in Chapters Four, Five, Seven, and Eight. Niche similarities among the

carnivore species varied according to the resources that were considered, which is what theory predicts. A high degree of similarity, such as large values of niche overlap, do not necessarily indicate competition unless those resources are in short supply (Levins 1968; Schoener 1974a; Jackson 1981). High overlap can exist because competition is absent (Vandermeer 1972; Sale 1974). The described niches show similarities and differential use of resources, without explaining whether those differences exist because of random variation, competition, other influences, or a combination thereof.

The three methods used to assess interspecific resource-use similarity are not designed to demonstrate the existence of competition, especially the interspecific interference competition detailed in Chapter Ten and the intraspecific competition in cheetah discussed in Chapter Eleven. Their value, however, is two-fold: They provide comparisons of how the carnivores are behaving relative to another when coexisting in the same environment; and they show ecological similarities that are likely to be foci of competition if resources are in short supply. For example, these species-niche descriptions identified lions as the closest thing to a "super-species" (sensu Tilman 1982:247); but this means that they are only potentially a superior competitor on more than one axis, not that they actually are.

The within-species patterns of differential resource utilization are described by working with individuals (Wiens 1974, 1977:593) or with sex, age, and social groups (e.g. cheetah in Chapter Eleven). The niche analyses of cheetahs were not extended to the level of individual animals, but instead compared the niches of various group types to

describe intraspecific similarities and differences in resource use. The potential for intraspecific competition probably is greater than it is for interspecific competition, because conspecifics are likely to be more similar in their multidimensional niches.

Niches described for the entire year, or even for season or locality, cannot show the occasional, intense, short-term bouts of interference competition, such as were described in Chapter Ten and Section 9.2.a. Hence, development of a management plan is not greatly assisted by the niche methods, and must rely on the other sources of information that I obtained.

Approaches that are too general fail to identify crucial events. The community models examined in Chapter Twelve are as inadequate as are niche descriptions as tools for wildlife management in the Serengeti ecosystem. Unlike the niche descriptions, these community models are supposed to have explanatory power for the effects of competition. None of the models, however, was substantiated by the Serengeti ecosystem's carnivore data, and the models provided little hint of the brief but important events of interference competition.

Evidence of interspecific and intraspecific competition came from direct observations of cleptoparasitism, harassment, and killing (Chapter Ten). And long-term studies made it possible to identify crucial competitive interactions, such as those which occur between spotted hyenas and African wild dogs on the Serengeti Plains in the dry season (Section 9.2.a). These competitive bouts are sufficiently severe to depress the African wild dog population, and to threaten the species with extinction in the ecosystem. These interactions, among and within species, clearly need to be understood to design an

effective management plan.

The species niche and community models may have basic value in broadening the understanding of species similarities, and in suggesting points where competition is likely to occur. But they have yet to be shown useful in identifying and solving specific management problems in the Serengeti ecosystem. In contrast, the direct observations and long-term studies identified some foci of competitive interactions that are of considerable importance for managing the carnivores. These results are considered along with other information to provide recommendations, in Section 14.4, for conserving carnivores in the Serengeti ecosystem.

14.5 Management Strategy for the Serengeti Carnivores

The Serengeti rapidly is becoming an isolated ecosystem, and in the future it is likely that management actions will be necessary if African wild dogs, cheetahs, and other vulnerable species are to be maintained.

The species most threatened with extinction, as pointed out by Fowler and MacMahon (1982), are those which are the predators, specialists, large-bodied mammals, and those which have small geographic ranges. Species with generalized feeding habits, e.g. the grey fox, are usually better at coping with altered habitats than are specialized feeders, e.g. the red fox (Hockman and Chapman 1983). By these criteria, the large Carnivora are the portion of the Serengeti's fauna that should be monitored most closely.

The luxury of allowing the flora and fauna within national parks and reserves to remain untouched, to do what they will, is fast

disappearing. Most parks are inadequate in size and are quickly becoming isolated from one another as intervening lands are transformed or developed by humans. In the Etosha ecosystem, Namibia, the construction of fences apparently caused a severe decline in the numbers of migratory wildebeest, which led to several major problems, including intensified competition between lions and cheetahs (Berry 1980, cited in Ferrar 1983:29). The problems associated with managing large mammals in Africa were reviewed in Ferrar (1983). Caro (1984) reviewed fallacies regarding sport hunting as a management technique.

A management plan for the Serengeti ecosystem's carnivores is needed to prevent the eventual extinction of some species. The rapidly growing human population around the ecosystem's periphery (Kurji 1976, 1979; Makacha et al. 1982) is imposing an island effect. In former times, occasional localized extinctions of vulnerable species occurred, but there was sufficient freedom of movement for dispersing individuals to colonize and repopulate. This widespread problem in East Africa was reviewed by Harris (1984), and a specific example was described for the nearby Tarangire National Park (Borner 1985).

One approach to solving the localized extinction problem is to translocate individuals from other parks and reserves as needed. The main disadvantage, however, is the loss of particular genetic stocks when races or localized populations perish. The translocation procedure has worked satisfactorily for white rhinos (Ceratotherium simum) in southern Africa (e.g., cf. Tomlinson 1977); however, reestablishment of wild Carnivora populations is less likely to be successful, because their considerable mobility likely will result in immediate travel that leads them out of protected areas (G. and L.

Frame 1981). In the Umfolozi Game Reserve, R.S.A., where lions were reestablished, there were problems of wandering by initial transplants and dispersal later from the established population (J.L. Anderson 1981). Captive-bred male cheetahs released in the R.S.A. became involved in a fight with resident cheetahs (Pettifer 1981a). And an attempt to increase cheetah numbers in Kruger National Park, R.S.A., resulted mostly in dispersal or death (Ferrar 1983:17). Captive-raised cheetahs released in the wild readily revert to dependency on humans (Pettifer 1981a; G. and L. Frame 1981).

A more sensible approach to conservation, therefore, seems to be the minimal and occasional application of selective corrective adjustments to the vegetation, herbivores, or carnivores. Although there are aesthetic and moral objections to this approach, it nevertheless makes the best ecological sense. Any management decisions should be made with regard for the consequences to the entire ecosystem, because components are intricately interrelated (e.g. F.H. Wagner 1977).

The simplest management attempts often are frought with unexpected complexities. For example, Smuts (1978b) described how removing lions in the Central District of Kruger National Park resulted in increased immigration, particularly of subadults, and apparent suppression of births and decreased cub survival. Prey-to-cheetah ratios were investigated by Pettifer (1981b), who concluded that cheetah management is complicated by the selection of very specific prey types. Examples of the complexities of vegetation-herbivore management in the Serengeti ecosystem were discussed by Sinclair and Norton-Griffiths (1982) and Pellew (1983).

In view of Verner's (1984) evaluation of the guild concept as a tool for managing bird populations, it is pertinent to ask if the ungulate-eaters, as an investigator-defined unit, has any management utility. Verner reviewed earlier works that suggested the possibility of monitoring the well-being of an entire guild of populations by simply studying one indicator species from that guild, but he concluded that only the use of an entire guild would be useful. He recommended using habitat as the foremost criterion in defining a guild of birds, but I consider food to be a more meaningful criterion for defining a guild of carnivores, which is why I have dealt with the ungulate-eaters.

Sufficient information is available to make several management recommendations for conserving selected carnivores in the Serengeti ecosystem. The literature review of observed aggressive, predatory, and competitive interactions among the Serengeti ecosystem's carnivores (Chapters Nine and Ten) provides the basis for developing these management guidelines. Further support and perspective were provided by the niche descriptions (Chapters Four, Five, Seven, Eight, and Eleven), community models (Chapters Twelve and Thirteen), and prey-predator densities and ratios (Chapter Six).

African wild dogs appear to be the most vulnerable of the large and medium-sized Carnivora in the Serengeti ecosystem. During years of excessive dry-season rainfall on the Serengeti Plains, greater numbers of spotted hyenas remained on the plains. Their effect was to kill many African wild dog pups, either indirectly through starvation or directly through predation (Chapter Nine). When the dry seasons are drier, the spotted hyenas must leave the plains and seek food in the

woodlands. Clearly, from the Serengeti Plains example and the Ngorongoro Crater situation (Chapter Nine), wherever spotted hyenas exist in high densities, they can have a devastating effect on African wild dogs.

African wild dogs apparently always exist in low densities. Thus the only way to assess the status of the wild dog populations accurately is to monitor the numbers and reproductive success of several selected packs in the Serengeti woodlands, on the Serengeti Plains, and in the Ngorongoro Highlands. It then would be obvious when selective removal of some of the spotted hyenas might be required in particular localities. Localized extinction of African wild dogs is not necessarily serious for conservation of the species, because it is likely that environmental conditions will change sufficiently within several years to permit the African wild dogs in the surrounding woodlands to recolonize those locations. Therefore, I do not recommend controlling numbers of any carnivore species until such time as human settlements completely surround the ecosystem and prevent all movement of carnivores in and out of the ecosystem. That time may arrive within several decades. Until then, more effort should be devoted to studying the natural dynamics of the animal and plant communities so there will be a better foundation for future management decisions.

If it is deemed desirable for managers to intervene to maintain populations of African wild dogs on the Serengeti Plains, for example, the situation should be monitored carefully to gather information of scientific value from the experiment. Probably only certain individual spotted hyenas are responsible for most of the cleptoparasitism on wild dogs. These individuals could be selectively removed (using

immobilization or any other means) by following the wild dogs during their hunts. This approach would be more costly than merely removing a prescribed larger portion of the spotted hyena population, but it has the advantage of minimizing the intervention by managers. However, it probably would cause an undefined, but directed (and perhaps disadvantageous for the spotted hyena), change in gene frequencies in the spotted hyena population.

Cheetahs are very secretive in most of their activities. They generally begin a hunt by stalking their prey. After a brief, highly-visible chase, they drag their prey under vegetation. Hiding while eating reduces the chance of being cleptoparasitized (Section 9.2.b), and seeking shady cover is probably also important in facilitating heat dissipation after the chase. The cheetah's daytime hunting also reduces the likelihood of being seen by other ungulate-eaters, because most of them are daytime sleepers. Vultures, however, usually are quick to arrive when a cheetah makes a kill. Cheetahs seem able to persist among large numbers of other carnivores as long as sufficient vegetative cover is available and suitably-sized prey exist.

Extensive burning of grasslands does not favor cheetahs. If grasslands must be burned, it should be done under prescribed conditions of cool-burning, in a mosaic, leaving about half the area with grasses at least 50 cm tall. This management practice is especially desirable in tourist areas, because it improves visibility and encourages regeneration and recruitment of scenic woodlands. Bushland too is favorable to cheetahs.

With adequate prey and cover, it is unlikely that other Carnivora

would become abundant enough to exterminate the cheetah population, because cheetahs are (or can be) very secretive (G. and L. Frame 1981). Numbers of all the ungulate-eating Carnivora are severely restricted by their own intraspecific aggression (Schaller 1972; Kruuk 1972a; Bertram 1973; Smuts 1978b; G. and L. Frame 1981; also, Section 10.3), as well as by interspecific killing (Section 10.2).

Most of the Serengeti's ungulate populations seem to be limited more by food supply than by predation, so a controlled-burning program could ensure that sufficient diversity is maintained in the vegetation to permit continued survival of all the ungulate species. Diverse habitats and diverse prey types will facilitate the persistence of all the Carnivora species. Even the vulnerable African wild dogs probably do well in a woodland or bushland environment, because it is difficult for competitors to find them.

Maintaining a high prey-to-predator ratio should help to minimize competition among the carnivores. The importance of providing a large prey base is often ignored or underrated. The populations of lion, spotted hyena, cheetah, black-backed jackal, and common jackal apparently were increasing on the Serengeti Plains in the mid-1970's, because of increased dry-season rainfall and more abundant prey. But the Carnivora numbers will probably not go very much higher, although huge increases in the ungulate-eating birds might be possible. In the Ngorongoro Crater the numbers of most ungulate-eating Carnivora generally are unchanging, although the leopard population trend is unknown, and African wild dogs have decreased. Although maintaining a high prey-to-predator ratio helps increase carnivore numbers to some extent, beyond that the social intolerance among carnivores intensifies

and increases their mortality. Management for the maintenance of all species in high numbers probably is best achieved by frequent, small-scale manipulations (cf. T.E. Miller 1982).

The stated goals in Chapter One were to describe the potential and actual competitive relationships among the Serengeti's carnivores, to evaluate several methods of assessing competition, and to provide management recommendations for conserving cheetahs, African wild dogs, and other carnivores. To varying degrees, these goals were achieved.

The fauna and flora of the Serengeti ecosystem provide an exceptional example of a complex and dynamic natural community. The carnivores discussed here are only a small part of that ecological and esthetic treasure, which is unsurpassed by any other ecosystem on earth. The Serengeti's economic value as a wildlife area exceeds, by far, any other alternative land use. In the face of rapidly growing human populations, the Serengeti cannot continue to exist much longer without increased educational, political, and management efforts by conservations worldwide.

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APPENDICES

Appendix A

Names of Mammals

The following are the common and scientific names of all the mentioned mammals living in the Serengeti ecosystem of East Africa. Nomenclature and arrangement follow Meester and Setzer (1971), except for asterisks which denote common names frequently used in East Africa.

Order Primates:

Olive baboon	Papio anubis J.B. Fischer, 1829
Blue monkey	Cercopithecus mitis Wolf, 1822
Vervet	Cercopithecus pygerythrus F. Cuvier, 1821

Order Pholidota:

Temminck's ground pangolin	Manis temminckii Smuts, 1832

Order Lagomorpha:

Cape hare	Lepus capensis Linnaeus, 1758
Crawshay's hare	Lepus crawshayi de Winton, 1899
Red rock hare*	Pronolagus rupestris A. Smith, 1834

Order Rodentia:

African porcupine*	Hystrix cristata Linnaeus, 1758
Common mole rat	Cryptomys hottentotus Lesson, 1826
Spring hare*	Pedetes capensis Forster, 1778
Unstriped grass mouse*	Arvicanthis niloticus Desmarest, 1822

Order Carnivora:

Bat-eared fox	Otocyon megalotis Desmarest, 1822
African wild dog*	Lycaon pictus Temminck, 1820
Side-striped jackal	Canis adustus Sundevall, 1846

Black-backed jackal	Canis mesomelas Schreber, 1775
Common jackal*	Canis aureus Linnaeus, 1758
Cape clawless otter	Aonyx capensis Schinz, 1821
Spotted-necked otter	Lutra maculicollis Lichtenstein, 1835
Ratel	Mellivora capensis Schreber, 1776
Striped polecat	Ictonyx striatus Perry, 1810
Two-spotted palm civet	Nandinia binotata Gray, 1830
African civet	Viverra civetta Schreber, 1778
Small-spotted genet	Genetta genetta Linnaeus, 1758
Large-spotted genet	Genetta tigrina Schreber, 1778 (sensu stricto)
Egyptian mongoose	Herpestes ichneumon Linnaeus, 1758
Slender mongoose	Herpestes sanguineus Rüppell, 1835
White-tailed mongoose	Ichneumia albicauda G. Cuvier, 1829
Marsh mongoose	Atilax paludinosus G. Cuvier, 1777
Banded mongoose	Mungos mungo Gmelin, 1788
Dwarf mongoose	Helogale parvula Sundevall, 1846
Aardwolf	Proteles cristatus Sparrman, 1783
Striped hyaena	Hyaena hyaena Linnaeus, 1758
Spotted hyaena	Crocuta crocuta Erxleben, 1777
Cheetah	Acinonyx jubatus Schreber, 1776
Lion	Panthera leo Linnaeus, 1758
Leopard	Panthera pardus Linnaeus, 1758
Wild cat	Felis libyca Forster, 1780
Serval	Felis serval Schreber, 1776
Caracal	Felis caracal Schreber, 1776
Order Tubulidentata	
Aardvark	Orycteropus afer Pallas, 1766

Order Proboscidea:	
African elephant	Loxodonta africana Blumenbach, 1797
Order Hyracoidea:	
Rock hyrax*	Procavia johnstoni Thomas, 1894
Bush hyrax*	Heterohyrax brucei Gray, 1868
Tree hyrax*	Dendrohyrax arboreus A. Smith, 1827
Order Perissodactyla	
Black rhinoceros	Diceros bicornis Linnaeus, 1758
Burchell's zebra	Equus burchelli Gray, 1824
Order Artiodactyla	
Bush pig	Potamochoerus porcus Linnaeus, 1758
Warthog	Phacochoerus aethiopicus Pallas, 1766
Hippopotamus	Hippopotamus amphibius Linnaeus, 1758
Giraffe	Giraffa camelopardalis Linnaeus, 1758
African buffalo	Syncerus caffer Sparrman, 1779
Sitatunga	Tragelaphus spekei Sclater, 1864
Bushbuck	Tragelaphus scriptus Pallas, 1766
Greater kudu	Tragelaphus strepsiceros Pallas, 1766
Lesser kudu	Tragelaphus imberbis Blyth, 1869
Eland	Taurotragus oryx Pallas, 1766
Red forest duiker	Cephalophus natalensis A. Smith, 1834
Common duiker	Sylvicapra grimmia Linnaeus, 1758
Bohor reedbuck	Redunca redunca Pallas, 1777
Mountain reedbuck	Redunca fulvorufula Afzelius, 1815
Waterbuck	Kobus ellipsiprymnus Ogilby, 1833
Roan antelope	Hippotragus equinus Desmarest, 1804
Oryx*	Oryx gazella Linnaeus, 1758

Blue wildebeest*	Connochaetes taurinus Burchell, 1823
Kongoni*	Alcelaphus buselaphus Pallas, 1766
Topi	Damaliscus lunatus Burchell, 1823
Impala	Aepyceros melampus Lichtenstein, 1812
Klipspringer	Oreotragus oreotragus Zimmermann, 1783
Kirk's dik dik	Madoqua kirki Günther, 1880
Oribi	Ourebia ourebi Zimmermann, 1783
Steenbok	Raphicerus campestris Thunberg, 1811
Suni	Neotragus moschatus von Dueben, 1846
Grant's gazelle	Gazella granti Brooke, 1872
Thomson's gazelle	Gazella thomsoni Günther, 1884

Appendix B

Names of Birds

The following are the common and scientific names of all the mentioned birds living in the Serengeti ecosystes of East Africa. Nomenclature and arrangement follow Britton (1980).

Family Struthionidae:

Ostrich	Struthio camelus L.

Family Ciconiidae:

Marabou	Leptoptilos crumeniferus Lesson
Yellow-billed stork	Mycteria ibis L.

Family Phoenicopteridae:

Lesser flamingo	Phoeniconaias minor Geoffrey
Greater flamingo	Phoenicopterus ruber L.

Family Anatidae:

Egyptian goose	Alopochen aegyptiacus L.

Family Accipitridae:

African white-backed vulture	Gyps africanus Salvadori
Rüppell's vulture	Gyps rueppellii Brehm
Hooded vulture	Neophron monachus Temminck
Egyptian vulture	Neophron percnopterus L.
Lappet-faced vulture	Torgos tracheliotus Forster
White-headed vulture	Trigonoceps occipitalis Burchell
Lammergeyer	Gypaetus barbatus L.
Bateleur	Terathopius ecaudatus Daudin

Tawny eagle	Aquila rapax Temminck
Martial eagle	Polemaetus bellicosus Daudin
Black kite	Milvus migrans Boddaert
Family Phasianidae:	
Grey-breasted spurfowl	Francolinus rufopictus Reichenow
Family Numididae:	
Helmeted guineafowl	Numida meleagris L.
Family Gruidae:	
Crowned crane	Balearica pavonina L.
Family Corvidae	
White-necked raven	Corvus albicollis Latham
Cape rook	Corvus capensis Lichtenstein

Appendix C

Data Sources

More than two decades of ecological research in the Serengeti ecosystem by scores of scientists has resulted in a considerable amount of data on the ecology and behavior of most large animal species, although there is less coverage of small animals and vegetation (cf. citations in Sinclair and Norton-Griffiths 1979). Most of these field studies were carried out by scientists working through the Serengeti Research Institute, with the approval of Tanzania's National Scientific Research Council.

The following sources were searched for carnivore resource-use data from the Serengeti ecosystem:

Lion--Initially studied by W. Kühme (1966); later studied by G.B. Schaller (1972) for the period 1966-69; B.C.R. Bertram (1973, 1975a, 1975b, 1976, 1978) for the period 1969-73; J.P. Elliott (1975), Elliott and Cowan (1978), and Elliott et al. (1977) for the period 1970-72; J. Hanby and D. Bygott (1979, 1982) for the period 1974-77. Also, see Bygott, Bertram, and Hanby (1979); Packer and Pusey (1982).

Spotted hyena--Initially studied by W.H. Matthews (1939). Later studied by H. Kruuk (1966, 1970, 1972a, 1972b, 1975a, 1975b) for the period 1964-68.

Cheetah--G.B. Schaller (1968, 1972:295-320) for the period 1966-69; B.C.R. Bertram (1978) for the period 1969-73; G. and L. Frame (1981), G.W. Frame (1984), G.W. Frame and L.H. Frame (in prep.) for the period

1973-78, and T. Caro (1982) for current studies.

Leopard--B.S. Wright (1960) and H. Kruuk and M. Turner (1967) for the period 1957-65; G.B. Schaller (1972:283-294) for the period 1966-69; B.C.R. Bertram (1978, 1982) for the period 1969-77.

Striped hyena--H. Kruuk (1976) for the period 1964-72.

African wild dog--R.D. Estes and J. Goddard (1967) for the period 1964-66; G.B. Schaller (1972:321-344) for the period 1966-69; J.R. Malcolm and H. van Lawick (1975) for the period 1967-72; L.H. Frame and G.W. Frame (1976), L.H. Frame et al. (1979), G. and L. Frame (1981), L.H. Frame (1985a, 1985b), L.H. Frame and G.W. Frame (in prep.), and J.R. Malcolm (in prep.) for the period 1973-78.

Black-backed jackal--J. Wyman (1967) for the year 1966; J. Lamprecht (1978a) for the period 1971-75; P.D. Moehlman (1978, 1979, 1983) for the period 1974-80.

Common jackal--J. Lamprecht (1978a, 1981) for the period 1971-75; P.D. Moehlman (1983) for the period 1974-79.

Side-striped jackal--virtually unstudied; see Dorst and Dandelot (1970).

Vultures, six species--H. Kruuk (1967), C.J. Pennycuick (1972), and D.C. Houston (1974a, 1974b, 1975a, 1975b, 1978, 1980) for the period 1964-71; G.W. Frame and L.H. Frame (in prep.) for the period 1974-78.

Tawny eagle and marabou stork--D.C. Houston (1980) for the period 1968-71; G.W. Frame and L.H. Frame (in prep.) for the period 1974-78.

Studies of these carnivores elsewhere in Africa provide comparative information. The data are for lion (Pienaar 1969; Rudnai 1973, 1974, 1979a, 1979b; Rodgers 1974b; Smuts 1976a, 1978b; Berry et al. 1981; van Orsdol 1982; Apps 1982), spotted hyena (Pienaar 1969; Lindeque and

Skinner 1982), cheetah (Pienaar 1969; McLaughlin 1970; Eaton 1974; Wrogemann 1975; P.H. Hamilton 1981; Labuschagne 1981; Holmes 1981; Pettifer 1981a, 1981b), leopard (P.H. Hamilton 1976, 1981; R.M. Smith 1978; Pienaar 1969), African wild dog (Pienaar 1969; Reich 1979, 1981), black-backed jackal (Bothma 1971; Sleicher 1973; Rowe-Rowe 1976, 1982, 1983; van der Merwe 1953a, 1953b, 1953c; Pienaar 1969), common jackal (Macdonald 1979; McShane and Grettenberger 1984), and vultures, tawny eagle, and marabou stork (Petrides 1959; Pomeroy 1973, 1975; G.D. Anderson and Horwitz 1979; Piper et al. 1981; Mundy et al. 1983).

Smaller carnivores are omitted from most of the analyses because their food resources are almost entirely different from those of the larger canrivores. Studies in the Serengeti ecosystem have included serval (Geertsema 1976, 1981), aardwolf (Kruuk and Sands 1972), ratel (G. and L. Frame 1977), bat-eared fox (Lamprecht 1979), and four species of mongooses (Rood 1975, 1978, 1983; Rood and Waser 1978; Waser 1980, 1981). Caracal, African wild cat, ratel, and zorilla are virtually unstudied in the Serengeti ecosystem, although there have been some studies in southern Africa (e.g. Grobler 1981; Smithers 1978; Skinner 1979; Stuart 1977; Rowe-Rowe 1978; Dorst and Dandelot 1970).

Eighteen herbivorous mammals provide most of the food consumed by the Carnivora and vultures in the Serengeti ecosystem. The main data sources are the following: Giraffe (R.A.P. Pellew 1983; D.M. Pratt and V.H. Anderson 1979, 1985), eland (Sinclair and Norton-Griffiths 1979), African buffalo (Sinclair 1977), Burchell's zebra (H. Klingel 1965; H. Klingel and U. Klingel 1966), blue wildebeest (Darling 1960; L.M. Talbot and M.H. Talbot 1963b; Estes 1966, 1969, 1976; McNaughton 1976), waterbuck (Sinclair and Norton-Griffiths 1979), kongoni (Duncan 1975),

topi (Duncan 1975), warthog (Sinclair and Norton-Griffiths 1979), impala (P.J. Jarman and M.V. Jarman 1973), Grant's gazelle (Estes 1967a; Walther 1972), Bohor reedbuck (Sinclair and Norton-Griffiths 1979), Thomson's gazelle (Brooks 1961; Walther 1964, 1969, 1973, 1974, 1977, 1978a, 1978b; Bradley 1976), Crawshay's hare (G.W. Frame and F.H. Wagner 1981), Cape hare (G.W. Frame and F.H. Wagner 1981), rock hyrax (Hoeck 1975), bush hyrax (Hoeck 1975), and unstriped grass mouse (Senzota 1982, 1983). Also, cf. Sinclair (1983).

The Serengeti ecosystem's avifauna was surveyed by Sinclair (1975) and Folse (1982). And reptiles were surveyed by Kreulen (1979).

Body weights and sizes from all of the included species are from Astley Maberly (1960), Guggisberg (1963), Robinette (1963), Ledger (1963, 1964), Lamprey (1964), McCulloch and L.M. Talbot (1965), L.M. Talbot and McCulloch (1965), Sachs (1967), Watson (cited in Kruuk and Turner 1967), V.J. Wilson (1968), Pienaar (1969), Dorst and Dandelot (1970), Rodgers (1974a), D.J. Anderson and Horwitz (1979), Sinclair and Norton-Griffiths (1979), and G.W. Frame and L.H. Frame (in prep.).

Appendix D

Behavioral Activities

The defined categories of mutually exclusive and exhaustive activities used in studying Carnivora in the Serengeti ecosystem are described in Table D.1. An instantaneous observation of the activity and the distance traveled during the preceding interval were recorded at 15-min intervals.

Table D.1 Behavioral-activity categories defined for the Serengeti Carnivora.

Symbol	Category	Description
R	Resting	Lying with head down.
A	Alert	Lying with head up or sitting motionless or standing motionless.
M	Maintenance	Non-social marking, self-grooming, scratching, yawning, tail-flicking, defecating, urinating, wallowing, sniffing, or exploring.
V	Vocalizing	Vocalizations that do not fit in other categories, e.g. lion roaring.
G	Movement	Changing position within the group perimeter.
T	Traveling	Non-concealed walking, trotting, or running outside the group perimeter.
S	Stalking	Prey-directed concealment, with or without movement, using cover; ambushing.
C	Chasing	Non-concealed prey-directed movement; rushing or running at prey before or after selecting an individual.
E	Eating	Mouth on food; includes killing.
D	Drinking	Mouth on water; includes standing, sitting, or lying if the animal has not stepped away from the drinking position.
N	Nursing	Mouth on nipple; includes asleep on nipple.

(continued)

Table D.1 (continued)

J	Regurgitation	Includes any kind of vomiting.
P	Social Play	Social pawing, chasing, stalking, or wrestling.
Q	Non-social Play	Solitary pawing, stalking, running, or climbing.
F	Friendly Social	Grooming, greeting, sniffing another individual, allo-marking, licking raindrops from one another.
H	Hostile Social	Agonistic behavior, aggression, threats, or avoidance.
I	Inter-specific Actions	Friendly or hostile behavior directed toward another species.
X	Sex	Mating behavior; active pre-, during, and post-copulatory behavior between an adult male and adult female.

Appendix E

Carnivora Counted During the Transect Surveys

These data are from the two surveys on the Serengeti Plains in May 1977 and October 1977 (Serengeti Research Institute 1977a, 1977b). Both surveys comprised the same 39 transects.

Table E.1 Frequency of occurrence of Carnivora within survey transects. Abbreviations: L = lion, H = spotted hyena, C = cheetah, B = black-backed jackal, J = common jackal, S = side-striped jackal, F = bat-eared fox, R = ratel, A = aardwolf.

Seasons	Species of Carnivora								
	L	H	C	B	J	S	F	R	A
Wet Season Transects:									
tw1	0	3	0	0	0	0	0	0	0
tw2	1	10	0	2	2	0	4	0	0
tw3	1	8	0	5	0	0	4	0	0
tw4	0	9	0	2	1	0	4	0	0
tw5	0	11	0	2	0	0	2	0	0
tw6	0	7	0	0	2	0	0	0	0
tw7	5	2	0	0	4	0	0	0	0
tw8	0	11	3	0	2	0	0	0	0
tw9	0	35	0	4	6	0	8	0	0
tw10	0	17	1	0	20	0	0	0	0
tw11	0	14	0	0	9	0	0	0	0
tw12	6	7	0	1	9	0	0	0	0
tw13	1	21	2	4	18	0	0	0	0
tw14	0	5	3	0	3	0	0	0	0
tw15	0	8	6	2	7	0	0	0	0
tw16	2	6	0	0	9	0	0	0	0
tw17	3	23	0	3	0	0	5	0	0
tw18	8	18	0	0	15	0	0	0	0

(continued)

Table E.1 (continued)

tw19	1	2	0	6	1	0	4	0	0
tw20	0	1	3	3	10	0	0	0	0
tw21	0	1	0	0	1	0	0	0	0
tw22	0	1	0	0	4	0	0	0	0
tw23	0	2	0	0	5	0	0	0	0
tw24	0	0	0	0	2	0	0	0	0
tw25	0	0	0	0	2	0	0	0	0
tw26	0	1	0	0	0	0	0	0	0
tw27	0	2	0	0	0	0	0	0	0
tw28	0	2	0	0	0	0	0	0	0
tw29	10	0	0	0	0	0	0	0	0
tw30	1	4	0	0	0	0	0	0	0
tw31	0	1	0	0	0	0	0	0	0
tw32	7	1	0	1	0	0	0	0	0
tw33	0	1	0	0	0	0	0	0	0
tw34	0	2	0	0	0	0	0	0	0
tw35	1	7	0	0	0	0	0	0	0
tw36	0	0	0	0	0	0	0	0	0
tw37	0	0	0	0	0	0	0	0	0
tw38	0	0	0	0	0	0	0	0	0
tw39	0	0	0	0	0	0	0	0	0
Season totals	47	243	18	35	132	0	31	0	0
Dry Season Transects:									
td1	0	2	0	2	2	0	0	0	0
td2	0	1	0	0	0	0	2	0	0
td3	0	1	0	0	1	0	0	0	0
td4	0	1	0	0	0	0	0	0	0
td5	0	1	0	1	1	0	0	2	0
td6	0	12	0	0	1	1	0	0	0
td7	0	1	0	0	2	0	0	0	1
td8	0	0	1	0	6	0	0	0	0
td9	0	1	0	0	6	0	0	0	0
td10	0	4	0	0	6	0	0	0	0
td11	1	0	0	0	11	0	0	0	0
td12	0	6	0	0	5	0	0	0	0
td13	0	0	0	0	8	0	0	0	0
td14	0	0	0	0	2	0	0	0	0
td15	0	1	0	0	5	0	0	0	0
td16	0	1	0	0	10	0	0	0	0
td17	0	4	0	2	1	0	0	0	0
td18	0	0	0	0	5	0	0	0	0
td19	0	0	0	0	1	0	0	0	0
td20	0	1	0	0	7	0	0	0	0
td21	0	2	0	0	2	0	0	0	0
td22	0	1	0	0	2	0	0	0	0
td23	0	0	0	0	2	0	0	0	0

(continued)

Table E.1 (continued)

td24	0	0	0	0	2	0	0	0	0
td25	0	0	0	0	2	0	0	0	0
td26	0	0	0	0	0	0	0	0	0
td27	0	0	0	2	0	0	0	0	0
td28	0	1	0	0	1	0	0	0	0
td29	3	0	1	2	0	0	1	0	0
td30	0	0	0	0	0	0	1	0	0
td31	0	2	0	0	0	0	0	0	0
td32	0	4	0	1	0	0	0	0	0
td33	0	4	0	0	0	0	3	0	0
td34	0	9	1	3	0	0	0	0	0
td35	0	1	0	0	0	0	0	0	0
td36	0	0	1	0	0	0	3	0	0
td37	0	0	0	0	0	0	0	0	0
td38	3	0	0	2	0	0	0	0	0
td39	0	0	2	0	0	0	0	0	0
Season totals	7	61	6	15	91	1	10	2	1

Appendix F

Foods of the Five Largest Carnivora

Food types that were caught, scavenged, or foraged by the five largest ungulate-eating Carnivora are summarized here. As far as possible the foods are listed by prey species. These records are from the following sources: Lion (Kruuk and Turner 1967: their Table 4; Schaller 1972: his Table 36; Elliott and Cowan 1978: their Table 3), spotted hyena (Kruuk 1972a: his Tables 11 and 12; J. Goddard, pers. comm., cited in Kruuk 1972a:64), cheetah (Kruuk and Turner 1967: their Table 6; Schaller 1972: his Table 63; G.W. Frame and L.H. Frame, in prep.), leopard (Kruuk and Turner 1967: their Table 5; Schaller 1972: his Table 63), and African wild dog (Estes and Goddard, 1967:58 and their Table 1; Kruuk and Turner 1967:18 and their Table 8; Kruuk 1972a: his Table 36; Schaller 1972: his Table 66; Malcolm and H. van Lawick 1975: their Table 2; and L.H. and G.W. Frame (unpubl. data).

Table F.1 Frequency of occurrence of food types eaten by the five largest Carnivora. Abbreviations: L = lion, H = spotted hyena, C = cheetah, P = leopard, D = African wild dog.

Food Types	Species of Carnivora				
	L	H	C	P	D
Giraffe	15	0	0	0	0
African buffalo	85	4	0	0	1
Eland	17	2	0	0	0

(continued)

Burchell's zebra	295	122	6	6	40
Blue wildebeest	504	468	38	16	346
Waterbuck	2	2	1	1	0
Kongoni	7	1	6	2	5
Topi	44	5	3	4	9
Warthog	22	4	0	1	13
Impala	6	1	9	9	4
Grant's gazelle	14	13	18	12	61
Bushbuck	1	0	0	1	1
Bohor reedbuck	10	0	5	25	0
Thomson's gazelle	359	165	372	119	488
Kirk's dik dik	0	0	3	0	0
Rock hyrax	0	0	0	1	0
Springhare	0	1	0	1	2
Hares	1	2	29	0	9
Pangolin	1	0	0	0	0
Lion	3	1	0	0	0
Spotted hyena	2	5	0	0	0
Ostrich chicks or eggs	6	1	0	0	8
Helmeted guinea fowl	1	0	1	1	0
Sandgrouse	1	0	0	0	0
Saddle-billed stork	1	0	0	0	0
Bat-eared fox	0	2	0	2	0
Common jackal	0	2	1	1	0
Puffadder	0	1	0	0	0
Python	0	1	0	1	0
Baboon	0	0	0	3	0
Porcupine	1	1	0	0	0
Black-backed jackal	0	0	0	2	0
Serval	0	0	0	2	0
Cheetah	0	0	0	1	0
Leopard	1	0	0	0	0
Secretary bird	0	0	0	1	0
European stork	0	0	0	6	0
Vulture	0	0	0	1	0
Caracal	0	0	1	0	0
Egyptian goose	0	0	1	0	0
Spurfowl	0	0	1	0	0
Wheatear	0	0	0	0	1
Domestic cattle	0	1	0	0	0
Placenta	0	3	0	0	0
Mouse	0	0	0	0	1
Beetles	0	0	0	0	7
Termites	0	3	0	0	2
Totals	1,399	811	495	219	998

Apppendix G

Resources Used by Five Types of Cheetah Groups During Hunts

Five kinds of cheetah groups were recorded using 80 resource states on nine niche axes during 495 hunts. The data are from the 1973 to 1978 field study of G.W. Frame and L.H. Frame.

Table G.1 Frequency of occurrence of resource use by five cheetah group types. Abbreviations: M = adult female alone or with cubs $\leq$ 10 mo. old, N = adult female with cubs > 10 mo. old, K = sub-adult littermates after leaving their mother, Q = adult male alone, T = adult males in a group.

Resource States	Cheetah Group Type					Total Number of Observations on Each Axis[1]
	M	N	K	Q	T	
Axis I: Prey Body Weight						
0 to 1 kg	3	1	0	0	0	
2	17	5	4	2	3	
3	7	1	2	0	4	
5	3	1	4	0	1	
6 to 10	7	4	0	1	3	
11 to 15	5	1	0	0	1	
16 to 20	105	20	11	3	12	
21 to 25	73	7	5	1	9	
26 to 30	0	0	0	1	2	
31 to 40	8	3	2	0	2	
41 to 50	12	5	1	0	10	
51 to 60	1	3	2	0	0	
61 to 70	4	2	1	0	3	
91 to 100	0	0	0	0	1	
101 to 150	4	2	1	0	14	
151 to 200	1	0	1	0	23	

(continued)

Table G.1 (continued)

201 to 300	0	5	0	0	4	
600	0	0	0	0	1	
						445
Axis II:						
Habitat Density						
Short grass	30	7	6	0	3	
Sh & med mosaic	119	26	10	7	62	
Med grass & herb	50	18	4	2	15	
Bushland	19	1	3	1	0	
Woodland	29	4	10	1	4	
						431
Axis III:						
Time of Hunting						
0401 to 0500 hr	0	1	0	0	0	
0601 to 0700 hr	15	4	4	1	3	
8 hr	42	7	6	2	7	
9	39	4	6	1	6	
10	28	4	3	0	4	
11	21	5	3	1	6	
12	16	5	0	2	8	
13	10	4	0	0	4	
14	7	4	1	2	5	
15	7	1	1	1	1	
16	6	2	1	0	5	
17	16	5	1	0	10	
18	13	3	2	0	4	
19	8	6	3	1	10	
20	1	0	0	0	2	
21	0	0	0	0	1	
						402
Axis IV:						
Species Hunted						
Hares	14	5	4	2	3	
Rodents	1	0	0	0	0	
Mongoose	2	0	0	0	0	
Caracal	1	0	0	0	0	
Jackal	1	0	0	0	0	
Zebra	0	8	1	0	10	
Warthog	1	2	1	0	1	
Eland	0	0	0	0	1	
Reedbuck	6	0	1	0	1	
Waterbuck	0	0	1	0	0	
Wildebeest	3	3	0	0	37	
Kongoni	2	1	0	1	1	
Topi	4	0	0	0	2	
Impala	1	1	1	1	0	
Dik dik	1	0	1	0	0	
Steenbok	0	1	0	0	0	

(continued)

Table G.1 (continued)

Grant's gazelle	21	7	3	0	10	
Thomson's gazelle	185	30	17	7	24	
Birds	5	2	2	0	2	
						443
Axis V:						
Prey Density						
None	0	2	0	1	0	
Few	30	15	9	1	4	
Moderate	121	25	7	2	10	
Abundant	57	6	3	2	6	
Migrations	11	0	7	0	10	
						329
Axis VI:						
Weather						
Sunny or clear	142	28	22	6	18	
Cloudy	51	16	6	0	12	
Rain	2	3	0	0	1	
						307
Axis VII:						
Prey Group Size						
1	74	14	8	4	14	
2	16	6	4	1	5	
3 to 5	18	3	2	0	6	
6 to 10	14	4	2	1	5	
11 to 20	10	5	1	1	4	
21 to 100	25	3	1	1	23	
101 plus	3	0	0	0	7	
						285
Axis VIII:						
Hunting Technique						
Stalking	135	30	12	5	35	
No stalking	34	12	4	2	13	
						282
Axis IX:						
Length of Chase						
Chase 0 to 10 m	10	2	0	0	0	
11 to 100 m	36	8	6	2	5	
101 to 300	29	10	3	2	2	
301 to 500	2	0	0	0	3	
501 to 1,000	2	0	1	0	0	
						123

1 Number of recorded observations out of a possible total of 495 on each resource axis.

Appendix H

Variables in Hunts by Lions, Cheetahs, and African Wild Dogs

Three species of large Carnivora are compared in their use of 34 occupied resource states on five axes during hunting. Lion data are from the following sources: Axis I (Schaller 1972:237, his Fig. 41), Axis II (Schaller 1972:237, his Fig. 40), Axis III (Schaller 1972: his Table 56), Axis IV (Schaller 1972:211, his Fig. 38), and Axis V (Schaller 1972:213, his Table 39). Cheetah data are from Appendices O and Q, with additional data on Axes I and II from Schaller (1972:315, his Fig. 44). African wild dog data are from Appendix Q, with additional data on Axes I and II from Schaller (1972:333, 337, his Fig. 44).

Table H.1 Frequency of occurrence of resource use during hunts by lion, cheetah, and African wild dog.

Resource States	Species of Carnivora		
	Lion	Cheetah	African Wild Dog
Axis I: Day Hunting Time			
0601 to 0700 hours	73	40	94
0701 to 0800 hr	129	94	113
9 hr	48	90	64
10 hr	29	59	14
11 hr	33	47	14
12 hr	19	37	9
13 hr	18	25	4
14 hr	19	26	1

(continued)

Table H.1 (continued)

15 hr	20	18	7
16 hr	22	21	8
17 hr	22	48	26
18 hr	33	36	70
19 hr	20	35	113
Totals	485	576	537
Axis II: Night Hunting Time			
1901 to 2000 hours	4	4	24
2001 to 2100 hr	3	1	6
22 hr	2	0	1
23 hr	1	0	4
24 hr	3	0	6
0001 to 0100 hr	3	0	3
02 hr	3	1	0
03 hr	6	0	1
04 hr	6	0	2
05 hr	1	1	0
06 hr	3	0	2
Totals	35	7	49
Axis III: Habitat Type			
Short grassland	65	46	121
Short & medium grasses	76	224	243
Medium grasses & herbs	25	89	28
Bushland	203	24	3
Woodland	85	48	17
Totals	454	431	412
Axis IV: Migratory Prey Eaten			
Zebra	83	4	1
Wildebeest	112	28	171
Thomson's gazelle	232	126	234
Totals	427	158	406
Axis V: Scavenged or Hunted			
Captured prey	885	209	408
Scavenged prey	193	1	27
Totals	1,078	210	435

Appendix I

Resemblance Matrices

This appendix contains the resemblance matrices from the cluster analyses of Chapters Four, Five, Seven, Eight, and Eleven. The cophenetic correlations show the agreement between each dendrogram and the corresponding resemblance matrix. Carnivora abbreviations: L = lion, H = spotted hyena, C = cheetah, P = leopard, D = African wild dog, B = black-backed jackal, J = common jackal, S = side-striped jackal, A = aardwolf, R = ratel, F = bat-eared fox. Vulture abbreviations: U = African white-backed, V = Rüppell's, W = lappet-faced, X = white-headed, Y = hooded, Z = Egyptian. Cheetah abbreviations: M = adult female alone or with cubs up to 10 months old, N = adult female with cubs older than 10 months, K = sub-adult littermate group that has separated from its mother, Q = solitary adult male, T = adult males in a group.

Table I.1 Resemblance matrix of nine Carnivora year-round. Calculated from the data in Appendix E. Cophenetic correlation = 0.872.

	Species							
Species	L	H	C	B	J	S	F	R
Spotted hyena	.122							
Cheetah	-.096	.148						
Black-backed jackal	.073	.441	.188					
Common jackal	.128	.400	.248	.032				
Side-striped jackal	-.046	.146	-.041	-.063	-.058			
Bat-eared fox	-.004	.554	-.093	.602	-.138	-.046		
Ratel	-.046	-.060	-.041	.028	-.058	-.014	-.046	
Aardwolf	-.046	-.060	-.041	-.063	-.030	-.014	-.046	-.014

Table I.2 Resemblance matrix of seven Carnivora year-round. Calculated from the data in Appendices F and J. Cophenetic correlation = 0.859.

	Species					
Species	L	H	P	C	D	B
Spotted hyena	.942					
Leopard	.602	.445				
Cheetah	.588	.430	.973			
African wild dog	.865	.816	.856	.863		
Black-backed jackal	.669	.514	.956	.989	.894	
Common jackal	.623	.471	.922	.954	.856	.966

Table I.3 Resemblance matrix of five Carnivora year-round. Calculated from the data in Appendix F. Cophenetic correlation = 0.744.

	Species			
Species	L	H	P	C
Spotted hyena	.934			
Leopard	.588	.407		
Cheetah	.574	.391	.974	
African wild dog	.860	.794	.856	.861

Table I.4 Resemblance matrix of lion, spotted hyena, cheetah, and African wild dog year-round. Calculated from the data in Appendix M. Cophenetic correlation = 0.974.

	Species		
Species	C	L	H
Lion	.918		
Spotted hyena	.928	.947	
African wild dog	.719	.631	.711

Table I.5 Resemblance matrix of six species of vulture year-round. Calculated from the data in Appendix T. Cophenetic correlation = 0.871.

	Species				
Species	U	V	W	X	Y
Rüppell's	.813				
Lappet-faced	.694	.897			
White-headed	.368	.444	.613		
Hooded	.661	.646	.519	.207	
Egyptian	.869	.782	.702	.442	.789

Table I.6 Resemblance matrix of nine Carnivora in the wet season. Calculated from the data in Appendix E. Cophenetic correlation = 0.860.

	Species							
Species	L	H	C	B	J	S	F	R
Spotted hyena	.014							
Cheetah	-.191	.093						
Black-backed jackal	-.054	.422	.148					
Common jackal	.118	.484	.315	.096				
Side-striped jackal*	.000	.000	.000	.000	.000			
Bat-eared fox	-.085	.605	-.183	.725	-.149	.000		
Ratel*	.000	.000	.000	.000	.000	.000	.000	
Aardwolf*	.000	.000	.000	.000	.000	.000	.000	.000

* None seen in the wet-season survey.

Table I.7 Resemblance matrix of nine Carnivora in the dry season. Calculated from the data in Appendix E. Cophenetic correlation = 0.866.

	Species							
Species	L	H	C	B	J	S	F	R
Spotted hyena	-.174							
Cheetah	.167	-.021						
Black-backed jackal	.437	.245	.194					
Common jackal	-.081	-.129	-.182	-.329				
Side-striped jackal	-.046	.666	-.062	-.082	-.081			
Bat-eared fox	.057	-.034	.194	-.089	-.293	-.059		
Ratel	-.046	-.042	-.062	.121	-.081	-.028	-.059	
Aardwolf	-.046	-.042	-.062	-.082	-.026	-.028	-.059	-.028

Table I.8 Resemblance matrix of lion, spotted hyena, cheetah, and African wild dog in the wet season. Calculated from data in Appendix M. Cophenetic correlation = 0.966.

	Species		
Species	C	L	H
Lion	.888		
Spotted hyena	.939	.954	
African wild dog	.722	.630	.710

Table I.9 Resemblance matrix of lion, spotted hyena, cheetah, and African wild dog in the dry season. Calculated from the data in Appendix M. Cophenetic correlation = 0.980.

	Species		
Species	C	L	H
Lion	.944		
Spotted hyena	.926	.917	
African wild dog	.739	.715	.778

Table I.10 Resemblance matrix of seven Carnivora in the Serengeti Plains location. Calculated from the data in Appendix W. Cophenetic correlation = 0.757.

	Species					
Species	L	P	C	H	D	B
Leopard	.609					
Cheetah	.603	.970				
Spotted hyena	.955	.602	.601			
African wild dog	.854	.841	.855	.913		
Black-backed jackal	.693	.441	.480	.711	.658	
Common jackal	.620	.802	.841	.613	.791	.724

Table I.11 Resemblance matrix of seven Carnivora in the Ngorongoro Crater location. Calculated from data in Appendix X. Cophenetic correlation = 0.910.

	Species					
Species	L	P	C	H	D	B
Leopard	-.067					
Cheetah	.243	-.042				
Spotted hyena	.973	-.058	.035			
African wild dog	.718	-.046	.821	.563		
Black-backed jackal	.877	-.099	.424	.821	.762	
Common jackal	.583	-.171	.565	.490	.697	.824

Table I.12 Resemblance matrix of the five largest Carnivora in the Serengeti Plains location. Calculated from data in Appendix W. Cophenetic correlation = 0.797.

	Species			
Species	L	P	C	H
Leopard	.600			
Cheetah	.598	.970		
Spotted hyena	.955	.594	.596	
African wild dog	.851	.839	.854	.912

Table I.13 Resemblance matrix of the five largest Carnivora in the Ngorongoro Crater location. Calculated from data in Appendix X. Cophenetic correlation = 0.905.

	Species			
Species	L	P	C	H
Leopard	-.092			
Cheetah	.233	-.057		
Spotted hyena	.972	-.080	.023	
African wild dog	.712	-.069	.820	.555

Table I.14 Resemblance matrix of five cheetah group types. Calculated from the data in Appendix G. Cophenetic correlation = 0.945.

	Group Type			
Group Type	M	N	K	Q
Adult female + cubs > 10 mo. old	.931			
Littermates	.876	.835		
Adult male alone	.868	.839	.792	
Adult males in groups	.612	.645	.486	.640

Appendix J

Foods of the Jackals

Black-backed jackals and common jackals are compared in their use of prey types that were caught, scavenged, or foraged. The jackal data are gleaned from Wyman (1967), H. and J. van Lawick-Goodall (1970:105-145), Kruuk (1972a:142-143), Schaller (1972:349), Lamprecht (1978a), and Moehlman (1983). Where a food was mentioned but no indication given of the number of times it was observed, it is tallied here as only one observation.

Table J.1 Frequency of occurrence of prey types hunted or eaten by black-backed jackal and common jackal.

Food Types	Number of Observations	
	Black-backed Jackal	Common Jackal
Zebra	2	2
Thomson's gazelle	23	15
Wildebeest	2	2
Springhare	0	3
Hare	4	1
Bat-eared fox	1	0
Common jackal	0	1
Unstriped grass mouse	1	1
Mice and rats	2	3
Striped sand snake	0	1
Unidentified snake	0	2
Lizard	0	1
Ground birds	1	2
Placenta	0	1
Termites	1	2
Beetles	1	3
Moth	0	1
Fruit	1	3
Mushroom	0	1
Totals	39	45

Appendix K

Scavengers of Cheetah-killed Prey

Observations of scavenging by lions, spotted hyenas, black-backed jackals, and common jackals were recorded during the cheetah field study of G.W. Frame and L.H. Frame (in prep.). Cases of cleptoparasitism and scavenging from cheetahs by the other Carnivora are listed here in all observations where the scavenger species were recorded. All of these observations were made in the Serengeti Plains study area.

Table K.1 Frequency of occurrence of scavenging from cheetah by other Carnivora.

Food Types	Number of Observations			
	Lion	Spotted Hyena	Black-backed Jackal	Common Jackal
Wildebeest	2	3	2	1
Zebra	0	1	0	0
Thomson's gazelle	10	22	23	7
Grant's gazelle	0	2	1	3
Impala	0	1	0	0
Hare	0	0	1	1
Totals	12	29	27	12

Appendix L

Foods Hunted and Scavenged by Five Carnivora in Two Locations

These observations are of lions, spotted hyenas, leopards, black-backed jackals, and common jackals eating captured or scavenged prey (G.W. Frame, unpubl. data). They occurred in and around the Serengeti Plains study area and in and around the Ngorongoro Crater study area. This summary does not repeat any of the data that are in Appendix K.

Table L.1 Frequency of occurrence of food types captured or scavenged by five species of Carnivora in two locations. Abbreviations: SP = Serengeti Plains, NC = Ngorongoro Crater.

Food Types	Number of Observations of Carnivora in Two Locations									
	Lion		Spotted Hyena		Leopard		Black-backed Jackal		Common Jackal	
	SP	NC	SP	NC	SP	NC	SP	NC	SP	NC
Elephant	0	0	1	0	0	0	0	0	0	0
African buffalo	5	3	2	1	0	0	0	0	0	0
Zebra	6	1	3	4	0	0	2	1	0	1
Eland	0	1	0	1	0	0	0	0	0	0
Thomson's gazelle	4	1	1	0	1	0	2	0	2	0
Wildebeest	4	1	3	3	0	0	3	2	0	1
Topi	0	0	0	0	1	0	0	0	0	0
Bushbuck	0	0	0	1	0	1	0	0	0	0
Bohor reedbuck	0	0	0	0	1	0	0	0	0	0
Bushpig	0	0	0	0	0	1	0	0	0	0
Porcupine	0	0	0	1	0	0	0	0	0	0
Aardvark	0	0	0	0	0	0	1	0	0	0
Dik dik	0	0	0	0	0	2	0	0	0	0
Hare	0	0	0	0	0	0	1	0	0	0
Common jackal	0	0	0	0	0	1	0	0	0	0
Egyptian goose	0	0	0	1	0	0	0	0	0	1
Lesser flamingo	0	0	0	1	0	0	0	0	0	0
Ostrich egg	0	0	1	0	0	0	0	0	0	0
Common mole rat	0	0	0	2	0	0	0	0	0	0
Domestic cow	0	1	0	0	0	0	0	0	0	0
Domestic donkey	1	0	0	0	0	0	0	0	0	0
Domestic goat	0	0	0	0	0	1	0	0	0	0
Human	1	0	0	1	0	0	0	0	0	0
Vervet	0	0	1	0	0	0	0	0	0	0
Fruit	0	0	0	1	0	0	0	0	0	0
Totals	21	8	12	17	3	6	9	3	2	3

Appendix M

Occurrence of Four Carnivora by Season

All lions, spotted hyenas, cheetahs, and African wild dogs that were seen during the transect surveys of hares from 12 July 1977 to 6 Febraury 1978 were recorded. No leopard was sighted. Each individual or group was considered as one sighting, and the resource states associated with the sighting are all those variables that were recorded for the hare survey. Details of the hare transect surveys were described by G.W. Frame and F.H. Wagner (1981).

Table M.1 Frequency of occurrence of variables associated with sightings of four species of Carnivora along hare survey transects in the wet and dry seasons.

Resource States	Number of Observations of Carnivora in Two Seasons								Total Number of Observations in Each Season	
	Lion		Spotted Hyena		Cheetah		African Wild Dog			
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Axis I:										
Diel Time										
Dawn	5	4	40	20	4	4	0	0		
Sunrise to 0900 hr	15	15	101	51	16	15	0	1		
0901 to 1200 hr	12	11	48	31	4	10	0	0		
1201 to 1500 hr	2	2	6	11	2	2	0	0		
1501 to sunset	5	8	18	8	6	4	2	2		
Dusk	2	0	10	5	0	0	1	0		
Postdusk to 2100 hr	3	0	10	3	0	0	0	0		
2101 to 2400 hr	0	0	2	3	0	0	0	0		
0001 to 0300 hr	0	0	1	3	0	0	0	0		
									315	213

(continued)

Table M.1 (continued)

Axis II:										
Habitat Type										
Short grass	1	1	7	2	0	0	0	0		
Sh grass/Solanum	2	2	15	3	0	1	1	0		
Sh grass/Hypoestes	0	0	18	0	4	0	0	0		
Sh gr/Indigof/Just.	0	3	28	16	2	3	1	1		
Med grass/P. mezi.	2	1	32	31	5	2	1	2		
Med gr/P. mezi./Ind.	0	1	1	2	0	2	0	0		
Med gr/T. triandra	11	8	39	43	10	11	0	0		
Woodland/riverine	28	24	91	38	11	16	0	0		
									310	213
Axis III:										
Weather										
Clear	22	38	158	117	22	32	2	2		
Cloudy	19	1	66	15	10	2	1	1		
Rain	1	1	8	2	1	1	0	0		
									310	212
Axis IV:										
Light at Night										
Moonlight	4	0	21	0	2	1	0	0		
No moon	4	0	39	23	1	2	0	0		
									71	26
Axis V:										
Condition of Grass										
Dry grass	0	11	0	17	1	14	0	1		
Slightly green grass	1	29	2	119	0	21	0	2		
Green grass	44	0	231	0	30	0	3	0		
									312	214
Axis VI:										
Water Availability										
None	4	18	23	98	9	24	1	2		
Puddles	8	0	61	3	5	2	0	0		
Waterholes	34	22	148	33	16	8	2	1		
									311	211
Axis VII:										
Gazelle Availability										
Thomson's gaz. none	10	5	45	6	10	10	1	1		
Thomson's gaz. few	14	27	82	89	9	24	2	2		
Thomson's gaz. many	20	8	101	43	12	1	0	0		
									306	216
Axis VIII:										
Wildebeest Availab.										
Wildebeest none	5	36	43	122	8	33	0	3		

(continued)

Table M.1 (continued)

Wildebeest few	15	8	81	14	17	2	1	0		
Wildebeest many	19	0	107	0	7	0	2	0		
									305	218
Axis IX:										
Hare Availability										
Hares none	36	37	197	115	30	35	3	3		
Hares present	8	2	31	15	3	1	0	0		
									308	208
Axis X:										
Ostrich Occurrence										
Ostriches none	24	26	142	88	20	19	2	3		
Ostriches present	20	14	91	48	13	16	1	0		
									313	214
Axis XI:										
Warthog Occurrence										
Warthogs none	19	20	123	87	21	20	3	3		
Warthogs present	24	19	110	48	12	16	0	0		
									312	213

Appendix N

Results of Three Methods of Calculating Multidimensional Niche Breadths and Overlaps for Four Carnivora, Year-round

Non-circular niche breadths and overlaps are calculated from the data on lion, spotted hyena, cheetah, and African wild dog in Appendix M. Data representing the entire year are obtained by combining the wet-season and dry-season observations. Calculations are first done on all 11 axes. Then the calculations are repeated using only Axes I through IV and VI through VIII, to see if deletion of axes that have questionable meaning substantially changes the results. The three methods used (product measure, summation measure, and projection on to single axes) are described in Section 3.3.c. The ecological interpretation is discussed in Section 5.5.

Results of the niche breadth analyses for the entire year are in Table N.1. And results of the niche overlap analyses are in Table N.2.

Table N.1 Mathematical results of three methods of calculating multidimensional niche breadths for lion, spotted hyena, cheetah, and African wild dog, year-round, using two data sets.

Niche Axes	Niche Breadths for Each Carnivora Species			
	Lion	Spotted Hyena	Cheetah	African Wild Dog
I	0.6899	0.6823	0.7206	0.4094
II	0.4947	0.7813	0.7433	0.4356
III	0.7295	0.7313	0.5812	0.9206
IV	1.0000	0.8803	1.0000	0.0000
V	0.8209	0.4869	0.9563	0.8864
VI	0.7997	0.9628	0.8173	0.7475
VII	0.9533	0.9224	0.9528	0.5218
VIII	0.9378	0.9829	0.7464	0.9808
IX	0.6856	0.7317	0.4522	0.0989
X	0.9825	0.9700	0.9899	0.7526
XI	0.9988	0.9900	0.9821	1.0000
Axes I to XI:				
Product	0.0983	0.1025	0.0761	0.0000
Summation	0.8266	0.8293	0.8129	0.6140
Projection	0.6976	0.7565	0.7332	0.4603
Axes I to IV and VI to VIII:				
Product	0.1780	0.2996	0.1809	0.0000
Summation	0.8007	0.8490	0.7945	0.5737
Projection	0.6804	0.7624	0.7257	0.5296

Table N.2 Mathematical results of three methods of calculating multidimensional niche overlaps for lion, spotted hyena, cheetah, and African wild dog, year-round, using two data sets. Abbreviationa: L = lion, H = spotted hyena, C = cheetah, W = African wild dog.

Niche Axes	Niche Overlaps for Each Dyad of Carnivora					
	LH	LC	LD	HC	HD	CD
I	0.9656	0.9875	0.8234	0.9480	0.6399	0.7539
II	0.9180	0.9568	0.3837	0.9802	0.4670	0.4605
III	0.9992	0.9919	0.9927	0.9963	0.9867	0.9660
IV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
V	0.9437	0.9822	0.9965	0.8750	0.9097	0.9933
VI	0.9649	0.9872	0.9350	0.9704	0.9910	0.9076
VII	0.9990	0.9721	0.5869	0.9628	0.4531	0.7929
VIII	0.9965	0.9915	0.9939	0.9512	0.9999	0.9164
IX	0.9999	0.9722	0.6433	0.9677	0.6014	0.8350
X	0.9994	0.9997	0.9403	0.9981	0.9529	0.9304
XI	0.9935	0.9897	0.9996	0.9996	0.9964	0.9935
Axes I to XI:						
Product	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Summation	0.8891	0.8937	0.7541	0.8772	0.7271	0.7772
Projection	0.9607	0.9757	0.7427	0.9701	0.8308	0.6197
Axes I to IV and VI to VIII:						
Product	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Summation	0.8347	0.8410	0.6737	0.8298	0.6482	0.6853
Projection	0.9471	0.9682	0.7761	0.9633	0.8343	0.6285

Appendix O

Prey Hunted by Lions, Cheetahs, and African Wild Dogs in Two Seasons

The numbers of lion-killed migratory prey are calculated by season from Schaller (1972:211-212, his Fig. 38).

Table O.1 Frequency of occurrence of migratory prey killed by lion in the wet and dry seasons.

Prey Species	Kills by Lion in Wet Season	Kills by Lion in Dry Season
Zebra	83	34
Wildebeest	112	28
Thomson's gazelle	232	222
Totals	427	284

The following comparison by season is of the prey species that were captured, killed, or eaten by cheetahs and African wild dogs, including scavenging. The cheetah data are from 212 successful hunts in which season and prey species were noted (G.W. Frame and L.H. Frame, in prep.); all of these hunts were on the Serengeti Plains and surrounding woodlands, except for one Thomson's gazelle that was caught inside the Ngorongoro Crater. The African wild dog data are from 455 successful hunts in which season and prey species were noted (L.H. and G.W. Frame,

unpubl. data); all of these hunts were on the Serengeti Plains or surrounding woodlands.

Table 0.2 Frequency of occurrence of the three main migratory prey and other prey hunted by cheetah and African wild dog in the wet and dry seasons.

Prey Species	Wet Season Hunts		Dry Season Hunts	
	Cheetah	African Wild Dog	Cheetah	African Wild Dog
Zebra	4	0	0	1
Wildebeest	25	140	3	31
Thomson's gazelle	60	120	66	112
Totals[1]	89	260	69	144
African buffalo	0	1	0	0
Kongoni	2	0	1	2
Topi	1	1	0	2
Warthog	0	1	0	0
Impala	4	1	2	0
Grant's gazelle	8	6	4	22
Reedbuck	3	0	0	0
Dik dik	1	0	1	0
Springhare	0	1	0	0
Hares	13	0	12	1
Common jackal	1	0	0	0
Birds	0	1	1	0
Beetles	0	5	0	2
Termites	0	2	0	0
Grasses	0	1	0	1
Cardboard	0	0	0	1
Totals	33	20	21	31

1 The three main migratory species.

Appendix P

Results of Three Methods of Calculating Multidimensional Niche Breadths and Overlaps for Lion, Cheetah, and African Wild Dog, Year-round

Circular niche breadths and overlaps are calculated from the data on three Carnivora in Appendix H. The three methods used (product measure, summation measure, and projection on to single axes) are described in Section 3.3.c. The ecological interpretation is discussed in Section 5.6.

Results of the niche-breadth analyses are in Table P.1. And results of the niche-overlap analyses are in Table P.2.

Table P.1 Mathematical results of three methods of calculating multidimensional, circular niche-breadths for three Carnivora, year-round.

Niche Axes	Niche Breadths		
	Lion	Cheetah	African Wild Dog
I	0.7971	0.9231	0.6566
II	0.8963	0.4363	0.4211
III	0.8657	0.6386	0.3915
IV	0.9397	0.3877	0.2859
V	0.8155	0.1271	0.4414
Product	0.4740	0.0127	0.0137
Summation	0.8629	0.5026	0.4393
Projection	0.5083	0.5627	0.4875

Table P.2 Mathematical results of three methods of calculating multidimensional, circular niche-overlaps for three Carnivora, year-round.

Niche Axes	Niche Overlaps		
	Lion & Cheetah	Lion & African Wild Dog	Cheetah & African Wild Dog
I	0.9602	0.8346	0.8353
II	0.6115	0.6729	0.8317
III	0.6778	0.4490	0.9176
IV	0.8266	0.6367	0.8876
V	0.6448	0.9388	0.8613
Product	0.2121	0.1507	0.4873
Summation	0.7442	0.7064	0.8667
Projection	0.7287	0.7786	0.9044

Appendix Q

Variables Associated with Cheetah and African Wild Dog Hunts

This comparison is of the 78 occupied resource states on nine axes for cheetahs during 495 hunts and for African wild dogs during 512 successful hunts. Data were recorded at all times of the year during the field studies of G.W. Frame and L.H. Frame (in prep.) and L.H. and G.W. Frame (unpubl. data).

Table Q.1 Frequency of occurrence of variables during hunts by cheetahs and African wild dogs.

Resource States[1]	Number of Observations		Total on Each Axis
	Cheetah	African Wild Dog	
Axis I: Habitat			
Short grass	46	121	
Short and medium grass	224	243	
Medium grass and herbs	89	28	
Bushland	24	3	
Woodland	48	17	
Totals	431	412	843
Axis II: Time of Hunt			
0001 to 0100 hours	0	2	
0201 to 0300 hr	0	1	
4 hr	0	2	
5 hr	1	0	
6 hr	0	2	
7 hr	27	66	

(continued)

Table Q.1 (continued)

8 hr	64	70	
9 hr	56	32	
10 hr	39	10	
11 hr	36	10	
12 hr	31	9	
13 hr	18	4	
14 hr	19	1	
15 hr	11	5	
16 hr	14	4	
17 hr	32	16	
18 hr	22	47	
19 hr	28	74	
20 hr	3	17	
21 hr	1	6	
22 hr	0	1	
23 hr	0	4	
2301 to 2400 hr	0	5	
Totals	402	388	790
Axis III: Prey Density			
None	3	2	
Few	59	21	
Moderate	165	89	
Abundant	74	170	
Migrations	28	123	
Totals	329	405	734
Axis IV: Weather			
Sunny or clear	216	161	
Cloudy	85	143	
Rainy	6	30	
Totals	307	334	641
Axis V: Prey Group Size[2]			
1	114	70	
2	32	8	
3 to 5	29	11	
6 to 10	26	8	
11 to 20	21	11	
21 to 100	53	43	
101 or more	10	66	
Totals	285	217	502
Axis VI: Hunting Technique[2]			
Stalking	217	87	
No stalking	65	164	

(continued)

Table Q.1 (continued)

Totals	282	251	533
Axis VII: Chase Length[2]			
0 to 10 meters	12	26	
11 to 100 m	57	22	
101 to 300 m	46	33	
301 to 500 m	5	25	
501 to 1,000 m	3	49	
1,001 m or more	0	80	
Totals	123	235	358
Axis VIII: Origin of Food			
Captured	209	408	
Scavenged	1	27	
Totals	210	435	645
Axis IX: Prey Species			
African buffalo	0	1	
Eland	1	0	
Zebra	19	1	
Wildebeest	43	171	
Kongoni	5	2	
Topi	6	3	
Waterbuck	1	0	
Warthog	5	1	
Impala	4	1	
Grant's gazelle	41	28	
Reedbuck	8	0	
Thomson's gazelle	263	234	
Steenbok	1	0	
Dik dik	2	0	
Springhare	0	1	
Hares	28	1	
Caracal	1	0	
Common jackal	1	0	
Mongooses	2	0	
Birds	11	1	
Rodents	1	0	
Beetles	0	7	
Termites	0	2	
Grasses	0	2	
Cardboard	0	1	
Totals	443	457	900

1 Some resource states were unrecorded during some hunts, so the number of resource states recorded is not the same on each axis.

2 For the African wild dog data these pertain only to captured prey.

Appendix R

Results of Three Methods of Calculating Multidimensional Niche Breadths and Overlaps for Cheetah and African Wild Dog, Year-round

Circular niche breadths and overlaps are calculated from the data of 495 hunts by cheetahs and 512 successful hunts by African wild dogs throughout the year. The three methods used (product measure, summation measure, and projection on to single axes) are described in Section 3.3.c. The ecological interpretation is discussed in Section 5.7.

Results of the circular niche-breadth and overlap analyses are in Table R.1.

Table R.1 Mathematical results of three methods of calculating multidimensional, circular niche breadths and overlaps for cheetah and African wild dog, year-round.

Niche Axes	Niche Breadths		Niche Overlaps of Cheetah and African Wild Dog
	Cheetah	African Wild Dog	
I	0.8808	0.6506	0.8290
II	0.7615	0.5603	0.7996
III	0.7961	0.8707	0.8513
IV	0.6148	0.8199	0.9521
V	0.7458	0.8577	0.7709
VI	0.8467	0.9564	0.8622
VII	0.4453	0.8797	0.4318
VIII	0.0716	0.5909	0.7628
IX	0.6570	0.4369	0.8297
Product	0.0043	0.0485	0.0976
Summation	0.6466	0.7359	0.7877
Projection	0.5295	0.5784	0.7969

Appendix S

Foods Eaten by Jackals in Two Seasons

The number of times that seven food types were found in the feces of black-backed jackals and common jackals are calculated from the data in Lamprecht (1978: his Table 2). The count data are listed separately for the wet and dry seasons.

Table S.1 Frequency of occurrence of food types in the feces of black-backed jackal and common jackal in the wet and dry seasons.

Food Types	Number of Observations			
	Black-backed Jackal		Common Jackal	
	Wet Season	Dry Season	Wet Season	Dry Season
Big ungulates	2	3	0	2
Small ungulates	17	15	9	4
Small mammals	1	4	5	3
Birds	0	3	1	0
Total arthropods	17	0	25	12
Total vegetable matter	21	18	13	6
Trash	1	2	1	0
Totals	59	45	54	27

Appendix T

Variables Associated With The Occurrence of Six Species of Vulture

The numbers of observations of the six species of vultures in the resource states along the ten niche axes were obtained from the following sources: The first six niche axes are of vultures observed scavenging from cheetahs during the field study of G.W. Frame and L.H. Frame (in prep.) The remaining four axes, and their published sources, are: Carcass parts scavenged (Kruuk 1967: his Fig. 2), sequence of arrivals (Kruuk 1967: his Fig. 3), number of other birds (Houston 1980: his Table 3), carcass size (Houston 1980: his Table 4). All the remaining categories include previously unpublished data on vultures observed scavenging from cheetahs during the field study of G.W. Frame and L.H. Frame (in prep.).

Table T.1 Frequency of occurrence of variables associated with six species of vulture, year-round. Abbreviations: U = African white-backed, V = Rüppell's, W = lappet-faced, X = white-headed, Y = hooded, Z = Egyptian.

Resource States	Number of Observations						Total on Each Axis
	U	V	W	X	Y	Z	
Axis I:							
Time of Day							
Sunrise to 0800 hours	2	2	3	0	1	1	
0801 to 1000 hours	6	4	7	2	4	0	
1001 to 1200 hours	4	2	2	0	2	0	
1201 to 1400 hours	2	1	1	0	1	0	
1401 to 1600 hours	2	2	1	1	0	0	
1601 hours to sunset	2	3	2	1	1	0	
Totals	18	14	16	4	9	1	62
Axis II:							
Habitat Density							
Short grass	1	1	1	0	0	0	
Short & medium mosaic	7	5	6	2	2	0	
Medium grass & herbs	6	4	5	1	4	0	
Bushland	1	3	3	0	2	0	
Woodland	2	1	1	1	0	1	
Totals	17	14	16	4	8	1	60
Axis III:							
Weather							
Sunny	11	9	11	2	5	1	
Cloudy	4	2	2	1	2	0	
Totals	15	11	13	3	7	1	50
Axis IV:							
Scavenging Birds							
Others present	13	13	12	4	6	0	
None present	5	1	4	0	3	1	
Totals	18	14	16	4	9	1	62

(continued)

Table T.1 (continued)

Axis V:							
Carnivora							
Present	13	11	14	2	8	0	
None present	5	3	2	2	1	1	
Totals	18	14	16	4	9	1	62
Axis VI:							
Arrival time							
0 to 5 min. after kill	0	1	1	0	0	0	
6 to 15 min.	6	4	3	1	4	0	
16 to 30 min.	1	1	2	0	0	0	
31 to 60 min.	5	1	4	0	1	0	
61 min. or later	5	5	5	4	2	1	
Totals	17	12	15	5	7	1	57
Axis VII:							
Parts Scavenged							
Soft meat	393	47	24	2	1	0	
Tear meat & skin strips	54	17	71	9	0	0	
Large scraps	0	0	4	8	2	0	
Tiny scraps	0	0	0	0	97	8	
Tear scraps off bones	0	0	0	0	8	10	
Totals	447	64	99	19	108	18	755
Axis VIII:							
Sequence of Arrivals							
Arrived first	6	0	3	10	0	1	
First five arrivals	33	0	19	16	2	4	
When maximum are present	892	195	126	14	112	56	
Last to leave	6	0	2	1	22	0	
Totals	937	195	150	41	136	61	1,520
Axis IX:							
Number of Other Birds							
None	0	1	2	5	0	0	
1 to 5 others	22	16	37	14	6	2	
6 to 20 others	93	76	83	14	13	11	
21 or more	112	111	54	4	36	8	
Totals	227	204	176	37	55	21	720
Axis X:							
Carcass Size							
0 to 10 kilograms	2	0	0	7	0	4	
11 to 20 kg	15	4	5	14	3	4	
21 to 150 kg	72	61	81	8	12	11	
151 to 300 kg	129	130	87	8	27	4	
301 kg or more	9	9	3	0	5	0	
Totals	227	204	176	37	47	23	714

Appendix U

Results of Three Methods of Calculating Multidimensional Niche Breadths and Overlaps for Vultures, Year-round

Non-circular niche breadths and overlaps are calculated from the vulture data in Appendix O, first using only Axes I through VI and then using all 10 axes. The three methods used (product measure, summation measure, and projection on to single axes) are described in Section 3.3.c. The ecological interpretation is discussed in Section 5.9.

Results of the two analyses of niche breadth by three methods are in Table U.1. And results of the two analyses of niche overlap by three methods are in Table U.2.

Table U.1 Mathematical results of three methods of calculating multidimensional niche breadths for six species of vulture, using two data sets.

Niche Axes	Niche Breadths for Each Vulture Species					
	African White-backed	Rüppell's	Lappet-faced	White-headed	Hooded	Egyptian
I	0.8991	0.9486	0.8141	0.5103	0.7461	0.1620
II	0.7742	0.8180	0.7965	0.6493	0.5042	0.2916
III	0.8988	0.7702	0.7123	0.9555	0.9178	0.2240
IV	0.8948	0.5519	0.8628	0.3483	0.9444	0.8387
V	0.8939	0.8179	0.6900	1.0000	0.6582	0.7565
VI	0.7766	0.7774	0.8953	0.2793	0.5905	0.1713
VII	0.3072	0.3959	0.3252	0.3582	0.2421	0.4950
VIII	0.2111	0.1167	0.3620	0.5555	0.2211	0.2470
IX	0.6502	0.5829	0.6816	0.8568	0.5474	0.6191
X	0.4550	0.3172	0.3157	0.8382	0.4203	0.8424
Axes I to VI:						
Product	0.3886	0.2097	0.2462	0.0308	0.1267	0.0012
Summation	0.8562	0.7807	0.7952	0.6238	0.7269	0.4074
Projection	0.7700	0.7079	0.7417	0.4810	0.6429	0.3528
Axes I to X:						
Product	0.0075	0.0018	0.0062	0.0044	0.0016	0.0001
Summation	0.6761	0.6097	0.6456	0.6351	0.5792	0.4648
Projection	0.2144	0.3587	0.3977	0.4934	0.3667	0.3764

Table U.2 Mathematical results of three methods of calculating multidimensional niche overlaps for six species of vulture, using two data sets. Abbreviations: U = African white-backed, V = Rüppell's, W = lappet-faced, X = white-headed, Y = hooded, Z = Egyptian.

Niche Axes	Niche Overlaps for Each Dyad of Vulture Species														
	UV	UW	UX	UY	UZ	VW	VX	VY	VZ	WX	WY	WZ	XY	XZ	YZ
I	.9799	.9615	.7921	.9455	.2906	.9658	.7204	.9206	.3700	.7012	.9546	.3714	.6638	.0000	.3228
II	.9460	.9508	.9335	.6843	.4886	.9982	.7708	.8666	.3032	.7630	.8884	.2682	.4369	.6925	.0000
III	.9893	.9788	.9961	.9996	.6389	.9982	.9724	.9850	.7402	.9571	.9729	.7899	.9981	.5623	.6171
IV	.9193	.9991	.7527	.9969	.8182	.9349	.9698	.8869	.5083	.7747	.9926	.7896	.7074	.0000	.8593
V	.9952	.9677	.9602	.9589	.7214	.9874	.9284	.9816	.6574	.8639	.9997	.4901	.8467	.8977	.4682
VI	.9231	.9439	.7264	.9397	.4457	.9334	.8187	.8982	.6238	.6202	.8906	.5384	.7241	.6299	.5751
VII	.9594	.7306	.5974	.0388	.0000	.8813	.7378	.0556	.0000	.9641	.0625	.0000	.0465	.0000	.0000
VIII	.9445	.9467	.6616	.9702	.9815	.8335	.2373	.9681	.9034	.8630	.8855	.9672	.4722	.7150	.9371
IX	.9960	.9489	.7826	.9937	.9933	.9391	.7452	.9932	.9825	.9393	.9193	.9599	.6799	.7973	.9829
X	.9626	.9746	.7015	.9844	.7596	.9871	.5869	.9741	.6102	.5565	.9768	.5744	.6445	.9201	.6900
Axes I to VI:															
Product	.7745	.8166	.3867	.5810	.0239	.8292	.3980	.6145	.0173	.2125	.7292	.0164	.1255	.0000	.0000
Summation	.9588	.9670	.8602	.9208	.5672	.9697	.8634	.9232	.5338	.7800	.9498	.5413	.7295	.4637	.4738
Projection	.9550	.9717	.8317	.9385	.6106	.9661	.8544	.9223	.5447	.7597	.9550	.5639	.7168	.4022	.5619
Axes I to X:															
Product	.6729	.5223	.0839	.0214	.0000	.5646	.0305	.0320	.0000	.0924	.0362	.0000	.0012	.0000	.0000
Summation	.9615	.9403	.7904	.8512	.6138	.9459	.7488	.8530	.5699	.8003	.8543	.5749	.6220	.5215	.5453
Projection	.9160	.8345	.6876	.7075	.5929	.9372	.8445	.8050	.7334	.9114	.7779	.6793	.6820	.6356	.9579

Appendix V

Results of Three Methods of Calculating Multidimensional Niche Breadths and Overlaps for Four Carnivora, by Season

Non-circular niche breadths and overlaps are calculated from the data for lion, spotted hyena, cheetah, and African wild dog in Appendix K. Calculations are first for the wet season and then the dry season. The three methods used (product measure, summation measure, and projection on to single axes) are described in Section 3.3.c. The ecological interpretation is discussed in Section 6.3.

Results of the niche-breadth analyses for the two seasons are in Table V.1. And results of the niche-overlap analyses for the same two seasons are in Table V.2.

Table V.1 Mathematical results of three methods of calculating multidimensional niche breadths for lion, spotted hyena, cheetah, and African wild dog in the wet and dry seasons.

Season	Niche Axes	Niche Breadths for Each Carnivora Species			
		Lion	Spotted Hyena	Cheetah	African Wild Dog
Wet	I	0.7532	0.6638	0.6321	0.3410
Wet	II	0.4717	0.7758	0.7464	0.4921
Wet	III	0.4163	0.8491	0.8784	0.9134
Wet	IV	1.0000	0.9586	0.9510	0.0000
Wet	V	0.0304	0.1345	0.0125	0.0035
Wet	VI	0.7559	0.7088	0.8976	0.7600
Wet	VII	0.9574	0.9713	0.9932	0.8645
Wet	VIII	0.9285	0.9348	0.9764	0.7985
Wet	IX	0.8304	0.7043	0.5615	0.1363
Wet	X	0.9960	0.9756	0.9772	0.9423
Wet	XI	0.9947	0.9986	0.9631	0.4647
	Product	0.0025	0.0249	0.0023	0.0000
	Summation	0.7395	0.7887	0.7809	0.5197
	Projection	0.6428	0.7133	0.7137	0.4641
Dry	I	0.5533	0.8096	0.5899	0.2944
Dry	II	0.4775	0.8678	0.6937	0.5057
Dry	III	0.3485	0.6915	0.9605	0.9949
Dry	IV	0.0000	1.0000	0.0000	0.0000
Dry	V	0.8986	0.6610	0.9856	0.9497
Dry	VI	0.1038	0.6517	0.8051	0.7546
Dry	VII	0.9673	0.8258	0.7268	0.5064
Dry	VIII	0.8540	0.6054	0.4119	0.1165
Dry	IX	0.4065	0.8116	0.2561	0.0754
Dry	X	0.9576	0.9597	0.9976	0.3926
Dry	XI	0.9998	0.9611	0.9946	0.4086
	Product	0.0000	0.0783	0.0000	0.0000
	Summation	0.5970	0.8041	0.6747	0.4544
	Projection	0.6219	0.7466	0.6328	0.4503

Table V.2 Mathematical results of three methods of calculating multidimensional niche overlaps for lion, spotted hyena, cheetah, and African wild dog in the wet and dry seasons. Abbreviations: L = lion, H = spotted hyena, C = cheetah, W = African wild dog.

Season	Niche Axes	Niche Overlaps for Each Dyad of Carnivora					
		LH	LC	LD	HC	HD	CD
Wet	I	0.9890	0.9445	0.6205	0.9340	0.2780	0.3300
Wet	II	0.9061	0.9055	0.3353	0.9522	0.5237	0.4795
Wet	III	0.9714	0.9822	0.9802	0.9996	0.9979	0.9985
Wet	IV	1.0000	1.0000	0.0000	0.0000	0.0000	0.0000
Wet	V	1.0000	0.3019	0.7493	0.7347	0.3512	1.0000
Wet	VI	0.9904	0.9335	0.8503	0.8999	0.9405	0.7596
Wet	VII	0.9993	0.9979	0.9176	0.9982	0.7721	0.9539
Wet	VIII	0.9945	0.9265	0.9823	0.9648	0.9352	0.4463
Wet	IX	0.9966	0.9749	0.5823	0.9909	0.6893	0.7940
Wet	X	0.9969	0.9973	0.9883	1.0000	0.9973	0.9969
Wet	XI	0.9969	0.9769	0.5811	0.9915	0.6828	0.7921
	Product	0.8486	0.2079	0.0000	0.0000	0.0000	0.0000
	Summation	0.9856	0.9037	0.6897	0.8605	0.6516	0.6864
	Projection	0.9702	0.9413	0.7453	0.9605	0.7335	0.6533
Dry	I	0.9394	0.9838	0.7870	0.9859	0.7930	0.8899
Dry	II	0.8035	0.9745	0.2234	0.8861	0.3575	0.2928
Dry	III	0.9357	0.6500	0.5244	0.9048	0.8458	0.9942
Dry	IV	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Dry	V	0.9662	0.9877	0.9967	0.9026	0.9386	0.9970
Dry	VI	0.8656	0.8426	0.9702	1.0000	0.9804	0.9831
Dry	VII	0.9856	0.7797	0.6011	0.4998	0.1681	0.9756
Dry	VIII	0.9900	0.9366	0.4966	0.9820	0.7161	0.8426
Dry	IX	0.9834	0.9828	0.7630	0.9184	0.4370	0.8737
Dry	X	1.0000	0.9932	0.7252	0.9937	0.7787	0.6070
Dry	XI	0.9890	0.9991	0.6073	0.9944	0.7725	0.6592
	Product	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
	Summation	0.8599	0.8300	0.6086	0.8243	0.6125	0.7377
	Projection	0.9014	0.9530	0.6760	0.9239	0.6646	0.6696

Appendix W

Foods of Seven Carnivora in the Serengeti Location

Prey species captured, scavenged, or eaten by the larger Carnivora on the Serengeti Plains and woodlands are extracted from the following sources: Lion (Kruuk and Turner 1967: their Table 4; Schaller 1972: his Table 36; Bertram 1982: his Figure 2; and Appendices K and L), spotted hyena (Kruuk 1972a: his Table 11; and Appendices K and L), cheetah (Kruuk and Turner 1967: their Table 6; Schaller 1972: his Table 63; and Appendix O), leopard (Kruuk and Turner 1967: their Table 5; Schaller 1972: his Table 63; Bertram 1982:349, his Figure 2; and Appendix L), African wild dog (Kruuk and Turner 1967: his Table 8; Schaller 1972: his Table 66; and Appendix Q), black-backed jackal (Wyman 1967; Schaller 1972:349; Kruuk 1972a:142; Lamprecht 1978a; Moehlman 1983; and Appendices K and L), and common jackal (Wyman 1967; Kruuk 1972a:142; Lamprecht 1978a; Moehlman 1983; H. and J. van Lawick-Goodall 1972:103-145; and Appendices K and L). Where a food type was mentioned without quantification, it is listed here as one observation.

Table W.1 Frequency of occurrence of food types captured, scavenged, or eaten by seven species of Carnivora on the Serengeti Plains and surrounding woodlands. Abbreviations: L = lion, H = spotted hyena, C = cheetah, P = leopard, D = African wild dog, B = black-backed jackal, J = common jackal.

Food Types	Number of Observations						
	L	H	C	P	D	B	J
Elephant	0	1	0	0	0	0	0
Giraffe	17	0	0	0	0	0	0
Buffalo	90	5	0	0	1	0	0
Eland	17	2	0	0	0	0	0
Zebra	296	72	5	6	12	4	3
Wildebeest	459	269	39	17	255	8	4
Waterbuck	2	1	0	3	0	0	0
Kongoni	11	1	6	2	3	0	0
Topi	46	5	3	6	7	0	0
Warthog	22	4	0	1	7	1	0
Impala	6	2	9	20	4	1	0
Grant's gazelle	13	9	18	12	41	2	5
Bushbuck	1	0	0	1	1	0	0
Bohor reedbuck	7	0	5	27	0	0	0
Thomson's gazelle	357	173	376	131	345	6	15
Dik dik	0	0	3	2	0	0	0
Rock hyrax	0	0	0	1	0	0	0
Springhare	0	1	0	1	1	0	1
Hares	1	1	29	2	2	6	3
Pangolin	1	0	0	0	0	0	0
Lion	3	0	0	1	0	0	0
Spotted hyena	2	0	0	1	0	0	0
Ostrich chick/egg	6	2	0	0	4	0	0
Guinea fowl	1	0	0	2	0	0	0
Sand grouse	1	0	0	0	0	0	0
Saddle-bill stork	1	0	0	0	0	0	0
Bat-eared fox	0	1	0	2	0	1	0
Common jackal	0	2	1	1	0	0	0
Python	0	0	0	1	0	0	0
Baboon	0	0	0	3	0	0	0
Porcupine	1	0	0	0	0	0	0
Black-backed jackal	0	0	0	5	0	0	0
Genet	0	0	0	1	0	0	0
Serval	0	0	0	2	0	0	0

(continued)

Table W.1 (continued)

Cheetah	0	0	0	2	0	0	0
Leopard	1	0	0	0	0	0	0
African Wild Dog	0	0	0	1	0	0	0
Aardvark	1	0	0	0	0	1	0
Secretary bird	0	0	0	1	0	0	0
European stork	0	0	0	6	0	0	0
Vulture species	0	0	0	1	0	0	0
Vervet	0	1	0	0	0	0	0
Starling sp.	0	0	0	1	0	0	0
Birds, unidentified	0	0	1	0	0	2	2
Dometic donkey	1	0	0	0	0	0	0
Placenta	0	2	0	0	0	1	1
Unstriped gr. mouse	0	0	0	0	0	1	0
Rodent, unidentif.	0	0	0	0	1	5	4
Snake, unidentified	0	0	0	0	0	0	1
Wheatear	0	0	0	0	1	0	0
Paper or cotton	0	0	0	0	1	1	1
Grasses	0	0	0	0	2	1	1
Duiker	0	0	0	1	0	0	0
Klipspringer	0	0	0	1	0	0	0
Steinbok	0	0	0	1	0	0	0
Fruits	0	0	0	0	0	3	2
Seeds	0	0	0	0	0	1	1
Dwarf mongoose	0	0	0	0	0	1	0
Wh.-tailed mongoo.	0	0	0	1	0	0	0
Hildebra. starling	0	0	0	0	0	1	0
Caspian plover	0	0	0	0	0	0	1
Crowned plover	0	0	0	0	0	0	1
Senegal plover	0	0	0	0	0	0	1
Frog, unidentified	0	0	0	0	0	1	0
Lizard, unidentif.	0	0	0	0	0	0	1
Sand and grit	0	0	0	0	0	1	1
Diplopoda	0	0	0	0	0	1	0
Centipedes	0	0	0	0	0	0	1
Dung beetles	0	0	0	0	7	3	6
Melolonthinae	0	0	0	0	0	1	1
Carebidae	0	0	0	0	0	1	0
Buprestidae	0	0	0	0	0	1	0
Beetles, unidentif.	0	0	0	0	0	1	1
Hodotermes	0	0	0	0	0	1	0
Termites, unident.	0	0	0	0	2	2	1
Crickets	0	0	0	0	0	1	1
Cockroaches	0	0	0	0	0	0	1
Tettigonidae	0	0	0	0	0	1	0
Acrididae	0	0	0	0	0	1	1
Muscidae	0	0	0	0	0	0	1
Insects, unidentif.	0	0	0	0	0	1	1
Spiders, unidentif.	0	0	0	0	0	1	1
Human	1	0	0	0	0	0	0
Totals	1,365	554	495	267	695	65	65

Appendix X

Foods of Seven Carnivora in the Ngorongoro Crater Location

Prey species that were recorded captured, scavenged, or eaten by the larger Carnivora inside the Ngorongoro Crater and in the surrounding montane forests and grasslands are extracted from the following sources: Lion (Elliott and Cowan 1978: their Table 3; and Appendix L), spotted hyena (Estes 1967b; Kruuk 1972a: his Table 12; and Appendix L), cheetah (Appendix O), leopard (Estes 1967b; and Appendix L), African wild dog (Estes and Goddard 1967), Black-backed jackal (Estes 1967b; Wyman 1967; Kruuk 1972a:142; H. and J. van Lawick-Goodall 1972:103-145; and Appendix L), and common jackal (Estes 1967b; Wyman 1967; Kruuk 1972a:142; H. and J. van Lawick-Goodall 1972:103-145; and Appendix L). Where a food type was mentioned without quantification, it is listed as one observation.

Table X.1 Frequency of occurrence of food types captured, scavenged, or eaten by seven species of Carnivora in the Ngorongoro Crater and surrounding montane forests and grasslands. Abbreviations: L = lion, H = spotted hyena, C = cheetah, P = leopard, D = African wild dog, B = black-backed jackal, J = common jackal.

Food Types	Number of Observations						
	L	H	C	P	D	B	J
Buffalo	4	2	0	0	0	0	0
Eland	3	1	0	0	0	0	0
Zebra	15	58	0	0	0	2	2
Wildebeest	58	208	0	0	18	5	4
Waterbuck	0	1	0	0	0	0	0
Kongoni	0	0	0	0	1	0	0
Grant's gazelle	1	6	0	2	4	0	0
Bushbuck	0	1	0	1	0	0	0
Bohor reedbuck	3	0	0	0	0	0	0
Thomson's gazelle	17	15	1	0	27	3	5
Dik dik	0	0	0	2	0	0	0
Bushpig	0	0	0	1	0	0	0
Springhare	0	0	0	0	1	0	1
Hares	0	1	0	0	1	0	0
Lion	0	1	0	0	0	0	0
Spotted hyena	0	5	0	0	0	0	0
Bat-eared fox	0	1	0	0	0	0	0
Common jackal	0	0	0	1	0	0	1
Jackal species	0	0	0	11	0	0	0
Puff adder	0	1	0	0	0	0	0
Porcupine	0	2	0	0	0	0	0
Lesser flamingo	0	1	0	0	0	0	0
Egyptian goose	0	1	0	0	0	0	1
Bird, unidentified	0	0	0	0	0	0	1
Domestic goat	0	0	0	1	0	0	0
Domestic cattle	1	1	0	0	0	0	0
Placenta	0	2	0	0	0	1	2
Common mole rat	0	2	0	0	0	0	0
Rodent, unidentif.	0	0	0	0	0	1	3
Striped sand snake	0	0	0	0	0	0	1
Snake, unidentif.	0	0	0	0	0	0	1
Hardware	0	5	0	0	0	0	0
Fruits	0	1	0	0	0	2	3
Dung beetles	0	0	0	0	0	0	2

(continued)

Table X.1 (Continued)

Insects, unident.	0	0	0	0	0	1	1
Grasshoppers	0	0	0	0	0	0	1
Crickets	0	0	0	0	0	0	1
Termites	0	3	0	0	0	0	1
Herbivore feces	0	0	0	0	0	0	1
Mushroom	0	0	0	0	0	0	1
Human	0	1	0	0	0	0	0
Totals	102	320	1	19	52	15	33

Appendix Y

Results of Three Methods of Calculating Multidimensional Niche Breadths and Overlaps for Five Types of Cheetah Groups, Year-round

Non-circular niche breadths and overlaps are calculated from the data of five group types of cheetah in Appendix S. The three methods used (product measure, summation measure, and projection on to single axes) are described in Section 3.3.c. The ecological interpretation is discussed in Section 8.2.

Results of the niche-breadth analyses are in Table Y.1. And results of the niche-overlap analyses are in Table Y.2

Table Y.1 Mathematical results of three methods of calculating multidimensional niche breadths for five group types of cheetah.

Niche Axes	Niche Breadths for Each Group Type of Cheetah				
	Adult Female Alone or With cubs < 10 mo. Old	Adult Female With cubs > 10 mo. Old	Sub-adult Litter-mates After Leaving Mother	Adult Male Alone	Adult Males in a Group
I	0.2449	0.3969	0.4722	0.2359	0.6191
II	0.7770	0.6160	0.8866	0.5714	0.4367
III	0.7112	0.8484	0.6117	0.5367	0.8324
IV	0.1958	0.5280	0.2572	0.1852	0.5109
V	0.5085	0.3540	0.7469	0.4596	0.7183
VI	0.6454	0.8670	0.5171	0.2011	0.6574
VII	0.6704	0.5608	0.4764	0.5525	0.7780
VIII	0.7935	0.9090	0.8678	0.9084	0.8928
IX	0.5243	0.2983	0.1887	0.1275	0.3263
Product	0.0024	0.0051	0.0020	0.0001	0.0123
Summation	0.5634	0.5976	0.5583	0.4198	0.6413
Projection	0.3982	0.4931	0.4028	0.2827	0.5575

Table Y.2 Mathematical results of three methods of calculating multidimensional niche overlaps for five group types of cheetah. Abbreviations: M = adult female alone or with cubs $\leq$ 10 mo. old, N = adult female with cubs > 10 mo. old, K = sub-adult littermates after leaving their mother, Q = adult male alone, T = adult males in a group.

Niche Axes	Niche Overlaps for Each Dyad of Cheetah Group Types									
	AB	AC	AD	AE	BC	BD	BE	CD	CE	DE
I	0.9124	0.8985	0.8527	0.6119	0.8774	0.8421	0.6842	0.8225	0.6299	0.5687
II	0.9777	0.9677	0.9441	0.9106	0.9011	0.9136	0.9406	0.8439	0.7256	0.9311
III	0.9593	0.9018	0.7969	0.9394	0.9056	0.8368	0.9853	0.8363	0.8511	0.8537
IV	0.8863	0.9363	0.9145	0.5050	0.8738	0.8058	0.8902	0.9594	0.7264	0.4444
V	0.7745	0.8405	0.7253	0.7933	0.3293	0.9570	0.6017	0.4436	0.9345	0.5533
VI	0.9828	0.9942	0.8062	0.9793	0.9649	0.6708	0.9973	0.8680	0.9399	0.7132
VII	0.9650	0.9310	0.9709	0.9569	0.9921	0.9940	0.8043	0.9753	0.7686	0.8178
VIII	0.9905	0.9965	0.9905	0.9933	0.9985	1.0000	0.9998	0.9985	0.9995	0.9998
IX	0.8035	0.7722	0.7638	0.7514	0.7154	0.7401	0.4886	0.9010	0.5451	0.6952
Product	0.4434	0.4395	0.2520	0.1467	0.1409	0.2450	0.1331	0.1882	0.1039	0.0451
Summation	0.9169	0.9154	0.8628	0.8268	0.8398	0.8622	0.8213	0.8498	0.7912	0.7308
Projection	0.9328	0.9013	0.8985	0.7927	0.8658	0.8398	0.8138	0.8550	0.7496	0.6415

VITA

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Doctor of Philosophy

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